

**CYTOLOGICAL CONDITIONS AND EVIDENCES
FOR HYBRIDITY IN NORTH AMERICAN
WILD ROSES**

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CYTOLOGICAL CONDITIONS AND EVIDENCES FOR HYBRIDITY IN NORTH AMERICAN WILD ROSES¹

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(WITH PLATES XVI-XIX AND FOUR FIGURES)



Introduction

Since the appearance of the outstanding papers of TÄCKHOLM (58, 59) on the cytology of *Rosa*, students of this perplexing genus have attempted to evolve satisfactory systems of classification of the multitudinous forms based on the varying chromosome numbers present (BLACKBURN AND HARRISON 4, HURST 31).

In previous studies on the cytology of our North American roses (TÄCKHOLM 59, PENLAND 46), the material has been obtained from the permanent collections in the various botanical gardens of Europe and the United States, the original stations for the material in the field being often unknown. It is not improbable that inter-specific crosses take place between the roses growing together in a large wild rose collection, and since the botanical gardens customarily supply one another with seeds taken from their growing plants, it is possible that after one or two generations of such dispersal some of the "wild species" in a garden may be forms entirely unknown in the field. In the autumn of 1922, the Botanical Garden of the University of Michigan began to build up a collection of North

¹ Papers from the Department of Botany of the University of Michigan, no. 299.

American wild roses from known stations in this continent; this was done with the kind cooperation of many collectors, who responded generously to our appeals and whose efforts make these studies possible. I am particularly indebted to several members of the United States Forest Service, and to Mr. CLYDE LEAVITT of the Board of Railway Commissioners for Canada. Mr. C. C. DEAM and Mr. C. C. EPLING have been most generous in sending interesting and critical forms during the past five years. This collection is intended to aid in the systematic study of *Rosa*, the American forms of which are, many of them, just as polymorphic as are the European types whose chromosome complexes reveal their hybrid nature.

Other workers have reported races within some species of *Rosa* possessing different chromosome numbers based on multiples of seven. TÄCKHOLM, for example, found *Rosa acicularis* Lindl. from Russia to be octoploid, but his Swedish material comprised both hexaploid and octoploid races. PENLAND's North European material was found to be hexaploid, as also Canadian material studied by HARRISON and BLACKBURN (27). TÄCKHOLM had some tetraploid specimens which ALMQUIST identified as *R. blanda* Ait.; PENLAND found *R. blanda* to be diploid. All the unquestionable forms of *R. cinnamomea* L. examined by TÄCKHOLM were diploid, whereas PENLAND (46) and HURST (32) place this species among the tetraploids. Although this is not an American species, it has escaped and has become established in several localities on this continent. The conclusion to be drawn from these findings is either that the chromosome number cannot be taken as a criterion for classifying *Rosa* forms, or else that the material has been incorrectly determined for the cytologists or by them.

In the present investigation many species have been examined cytologically from several parts of their natural ranges. A search was made for wild hybrid forms showing unpaired chromosomes, examples of which have not before been reported in American material. Artificial crosses have been made successfully between forms which differ in chromosome number. Unfortunately *Rosa* is a very unsatisfactory subject for genetical studies, both because of the difficulty in germinating the bony achenes, and because, except in a few Asiatic species, it takes three years for plants to reach maturity.

Material and methods

All the material for cytological study was taken from plants in the Botanical Garden of the University of Michigan, except material from a dozen early-flowering individuals which was kindly fixed by Dr. L. E. WEHMEYER in 1926 from plants in the Arnold Arboretum. The rose collection at Michigan was started at the end of 1922; few plants produced an abundance of flowers until 1926. Fixation was usually carried out in the afternoon, and meiosis was found to be just about as frequent on dull as on sunny days. Following the advice of Professor J. W. H. HARRISON and of Dr. C. C. HURST, the buds were fixed in Carnoy's solution. This fixing fluid has the advantage of rapid penetration, which is important in *Rosa* because the buds are fixed after merely slicing off the apex and base. Carnoy's solution causes a good deal of shrinkage, however, and in the summer of 1927 acetic-alcohol without chloroform was used, at the suggestion of Professor W. P. THOMPSON, who found that this gave a better result in his wheat material than Carnoy's solution. The acetic-alcohol swells the chromatin somewhat, facilitating observations. THOMPSON's method (60) of examining the fixed material after it has stood in 85 per cent alcohol, staining in bulk with acetocarmine, was tried. Although this method does not permit counts to be made, it enables buds in the reduction stage to be picked out before imbedding, thus saving unnecessary cutting.

Flemming's strong mixture, Zenker's solution, and Allen's modification of Bouin's fluid have also been tried. They all give less shrinkage than Carnoy's solution, but the penetration is poor. After these fixing fluids Haidenhain's iron-alum haematoxylin gives better results than after Carnoy's solution, when it sometimes fails to present good contrasts. The modification of Gram's stain as described by CLAUSEN (9) has been found very satisfactory, as has also plain gentian violet, particularly in the case of hybrid forms the protoplasts of which become much distorted by fixation.

For convenience prior to imbedding acetic-alcohol as a killing fluid is recommended, followed by staining with gentian violet; for detailed cytological studies in *Rosa*, strong Flemming or Allen's Bouin solution should be used, followed by iron-alum haematoxylin.

The fixed material was imbedded in paraffin. Sections of diploid

and triploid forms were cut 10–12 μ in thickness, those of tetraploids and higher polyploids at 12–14 μ , thus allowing some complete cells to appear on the sections and facilitating the counting of chromosome numbers.

Polyploid series

All North American wild roses heretofore examined cytologically fall into three groups: (1) the numerous diploid forms with fourteen somatic chromosomes and seven pairs at diakinesis; (2) the tetraploid group comprising *R. virginiana*, *R. carolina*,² *R. arkansana* and their allies, which have twenty-eight somatic chromosomes and fourteen pairs at diakinesis; (3) the *acicularis-nutkana* group which is hexaploid with forty-two somatic chromosomes and seven pairs at diakinesis. I have discovered an octoploid rose and also a few triploid and aneuploid forms on this continent.

RELATIVE CELL SIZES IN ROSA

TÄCKHOLM noticed that the size of microsporocytes at the stage of diakinesis is greater the larger the number of chromosomes, although he did not publish any measurements. The size of individual chromosomes appeared to him to be the same in all the forms of *Rosa*. Table I gives the diameter of microsporocytes measured at diakinesis. Four species or varieties from each group were selected from among diploid, tetraploid, and hexaploid species. These few measurements bring out the fact that diploid types have the smallest cells and hexaploids the largest, although there is considerable overlapping between the cell sizes at diakinesis in tetraploids and hexaploids.

Chromosome numbers

All the forms examined cytologically during the present study are included in the following list (table II). They are arranged according to their chromosome numbers, related types being grouped together in each class. The first column gives the species, accession number, and name of the original collector with date of collection.

² Cytologists should note the nomenclatorial confusion regarding *R. carolina* L. 1753, which is the correct name for *R. humilis* Marsh.; the name has unfortunately appeared in cytological literature as a synonym for *R. palustris* Marsh., the diploid species of the swamps of eastern North America (see RYDBERG 49, and FERNALD 22).

The second column gives the source of the material, usually the field collector's data. The third column contains the number of bivalent chromosomes at first reduction division; in the case of hybrid forms the number of unpaired, univalent, chromosomes present at diakinesis is placed after the number of bivalent chromosomes. The last column gives the number of chromosomes observed in somatic pro-phases. In the first column and immediately following the species

TABLE I

DIAMETER OF MICROSPOROCTES AT DIAKINESIS

SPECIES AND ACCESSION NUMBER*	TYPE	KILLING SOLUTION	LARGEST DIAMETER OF CELLS IN μ
<i>Rosa blanda</i> 3595.....	Diploid	Carnoy's	6.4
<i>R. pisocarpa</i> 4634.....	"	Carnoy's	7.2
<i>R. palustris</i> 4412.....	"	Allen's Bouin	7.2
<i>R. michiganensis</i> 5891.....	"	Carnoy's	7.2
<i>R. brachycarpa</i> 5301.....	Tetraploid	Allen's Bouin	9.6
<i>R. myriantha</i> 3537.....	"	Carnoy's	9.6
<i>R. obovata</i> 2751.....	"	Allen's Bouin	8.0
<i>R. carolina</i> 5808.....	"	Carnoy's	8.0
<i>R. engelmanni</i> E5.....	Hexaploid	Carnoy's	8.8
<i>R. acicularis</i> var. <i>lacorum</i> 6007.....	"	Carnoy's	9.6
<i>R. acicularis</i> var. <i>rotunda</i> 3511.....	"	Strong Flem- ming	11.2
<i>R. acicularis</i> E3 (European).....	"	Carnoy's	9.6

* Wherever "accession number" is referred to, the reference is to the serial accession numbers of the Botanical Garden of the University of Michigan. "Arn. Arb." numbers are those of the Arnold Arboretum. Nos. E 1, E 2, etc., are my cytological collection numbers for material fixed at the Arnold Arboretum.

name there are small letters which refer to the various kinds of meiotic irregularities observed. The key to these notations is placed at the head of the list.

Extrusion of chromatin has been observed in many cytological preparations of the sporocytes of plant genera. Chromatin or chromosomes are sometimes extruded into the cytoplasm, as found by TISCHLER (61), YASUI (67), LONGLEY (41), HURST (31); or chromatin may pass through the wall into an adjacent sporocyte, as shown by DIGBY (16) in *Galtonia candicans*, by GATES (24) in *Oenothera gigas*, and by WEST and LECHMERE (64) in *Lilium candidum*. This has been observed frequently in my material, especially in the prophase stages of meiosis (figs. 6, 15, 51), and is indicated by letter *b* in the first column. The significance of the phenomenon is

not understood, but it is regarded by several cytologists (TISCHLER 62, SAKAMURA 50) as being an indication of degeneration. Recently HURST (31) has used the occurrence of chromosome extrusion in *Rosa* as an argument in support of his theory of the origin of rose types with lower chromosome numbers from the higher polyploids.

In some roses it has been observed that occasionally a microsporocyte will give rise to only two spores (diad) instead of the normal four (tetrad) after meiosis. This has been indicated by *h* in table II.^{2a}

Cytological results

DIPLOID SPECIES

Rosa bracteata Wendl.—This rose, belonging to the small Asiatic section *Bracteatae*, was not obtained by TÄCKHOLM for his extensive studies. It has become thoroughly naturalized in southeastern United States, where it is common. A plant collected in northwestern Mississippi and grown in the greenhouse proved to be diploid, with seven pairs at diakinesis (fig. 1).

Rosa setigera Michx.—The single American representative of the section *Synstylae* is very constant in its morphological characteristics, varying chiefly in the amount of pubescence on the foliage. A specimen of the pubescent var. *tomentosa* T. & G. (*R. rubifolia* R. Br.) from Ohio confirmed TÄCKHOLM's observation, showing seven pairs at diakinesis.

Rosa gymnocarpa Nutt.—This species, reported by TÄCKHOLM to have fourteen somatic chromosomes, was found to have seven pairs at the first meiotic division (fig. 2). Material has not yet been obtained from any other member of the section *Gymnocarpae*.

Rosa palustris Marsh.—The tall swamp rose of eastern and southeastern North America is diploid, as has already been shown by others. It is the largest rose in Michigan, excepting *R. setigera*, and

^{2a} LIST OF CHROMOSOME NUMBERS.—*Explanation of notations:* (a) affinity between members of some pairs at first meiotic reduction weak, resulting in some univalent chromosomes at first anaphase (fig. 20); (b) much extrusion present in material; (c) two ovules observed in one ovary; (d) lagging of some chromosomes at meiotic anaphases (figs. 54, 59); (e) polyspory observed at tetrad stage of microsporogenesis (fig. 48); (f) meiosis not synchronous in sporocytes of one microsporangium; (g) rings of four chromosomes observed (figs. 39, 46); (h) diad groups found among tetrads of pollen (fig. 32).

TABLE II

SPECIES, ACCESSION NO., AND ORIGINAL COLLECTOR	ORIGIN	HAP- LOID NO.	SO- MATIC NO.
	DIPLOID TYPES		
R. bracteata Wendl. 3676, L. E. Wehmeyer, 1923.....	Miller, De Soto Co., Miss.	7	
R. setigera Michx. 3585, unknown.	Ohio	7	
R. gymnocarpa Nutt. 4006, C. C. Epling, 1923.....	Priest River, Idaho	7	
<i>Cinnamomeae</i>			
R. cinnamomea L. (b) 6082, Moses Gomberg, 1924.....	Keene Valley, Essex Co., N.Y.	7	
R. pisocarpa A. Gray 4634, R. M. Reid, 1923.....	Castella, Shasta Co., Calif.	7	
R. salicetorum Rydb. 3530, Ehlers and Erlanson, 1923.....	Copeland, Boundary Co., Idaho	7	
R. puberulenta Rydb. 5594, E. G. Wieschuegel, 1924.....	Wyo. Natl. For., Sublette Co., Wyo.	7	
R. macounii Greene 3820, S. Dowding, 1923.....	Edmonton, Alberta	7	14
R. woodsii Lindl. 3298 (plant D), F. B. Cotner, 1923.....	Bozeman, Gallatin Co., Mont.	7	14
R. woodsii Lindl. (a) (e) 4477 (plant N4) Edine Binney, 1923.	Fort Pierre, Stanley Co., S.D.	7	14
R. woodsii Lindl. (b) 3255, A. O. Garrett, 1923.....	Salt Lake Co., Utah	7	
R. woodsii Lindl. 8152, C. O. Erlanson, 1925.....	So. of Canyon City, Fremont Co., Colo.	7	14
R. pyrifera Rydb. (e) (f) 6610 (2 individuals), A. O. Garrett, 1925	Salt Lake Co., Utah	7, 8	14, 16
R. ultramontana Wats. 5293, W. H. Ransome, 1924.....	Spokane Co., Wash.	7	
R. fendleri Crépin (a) 3298 (plant A), F. B. Cotner, 1923.....	Bozeman, Gallatin Co., Mont.	7	
R. fendleri Crépin 5679, E. L. Perry.....	Santa Fé Natl. For., Sandoval Co., N.M.	7	
R. hypoleuca W. & S. 8154, C. O. Erlanson, 1925.....	Arkansas River, Fremont Co., Colo. (alt. 5500 ft.)	7	14
R. granulifera Rydb. (b) 5925, W. A. Archer, 1924.....	Black Creek, Sierra Co., N.M.	7	
R. subblanda Rydb. 3608, L. E. Wehmeyer, 1923.....	Roanoke, Huntington Co., Ind.	7	
R. blanda Ait. (d) (e) 4071, H. H. Bartlett, 1923.....	St. Ignace, Mackinac Co., Mich.	7	
R. blanda Ait. 3505, E. W. Erlanson, 1923.....	Bliss Woods, Kane Co., Ill.	7	
R. blanda Ait. 3942, H. H. Bartlett, 1923.....	Lakeland, Livingston Co., Mich.	7	
R. blanda var. hispida (d) 5771 (plant B), C. G. Harrold, 1924..	Gimli, Lake Winnipeg, Manitoba	7	

TABLE II—*Continued*

SPECIES, ACCESSION NO., AND ORIGINAL COLLECTOR	ORIGIN	HAP- LOID NO.	SO- MATIC NO.
<i>R. blanda</i> var. <i>hispida</i> (a) (b) (d) 5773, C. G. Harrold, 1924.....	Gimli, Lake Winnipeg, Manitoba	7	
<i>R. blanda</i> var. <i>hispida</i> (d) 2681, E. S. Reynolds, 1922.....	Agric. College, Cass Co., N.D.	7	
<i>R. blanda</i> var. <i>hispida</i> 2693, Helen Stegenger, 1922.....	University, Grand Forks Co., N.D.	7	
<i>R. blanda</i> var. <i>hispida</i> 4167, A. H. W. Povah, 1923.....	Beach, Cook Co., Ill.	7	
<i>R. blanda</i> var. <i>hermanni</i> 2686, F. J. Hermann, 1922.....	Laurium, Houghton Co., Mich.		14
<i>R. blanda glandulosa</i> (a) (b) (d) (e) 3753, J. H. Ehlers, 1923....	Prentis Bay, Mackinac Co., Mich.		
Parent plant B.....		7	14
2/N38.....		7	
5/N3.....		7	
7/N25.....		7	
7/N36.....		7	
Seedling plant { 7/N37.....		8	16
7/N57.....			14
7/N62.....			14
9/N1.....		7, 8	15
9/N9.....		7	
<i>R. michiganensis</i> (b) (c) (d) (e) 5890, E. W. Erlanson, 1924....	Douglas Lake, Cheboygan Co., Mich.	7	
<i>R. acicularioides</i> (a) (d) (e) 8261, H. H. Bartlett, 1925.....	Ogdensburg, St. Lawrence Co., N.Y.	7	14
<i>R. schuettea</i> (d) (e) 5891, C. and E. Erlanson, 1924.....	Douglas Lake, Cheboygan Co., Mich.	7	
<i>R. palustria</i> Marsh. 4412, E. E. Gunther, 1923.....	Spider Lake, Grand Travers Co., Mich.	7	
<i>R. palustris</i> var. <i>inermis</i> (b) (d) (e) 5714, H. H. Bartlett, 1924.....	Quanicassee, Saginaw Bay, Mich.	7	
<i>R. foliolosa</i> alba (d) (e) 9525, Ralph Shreve, 1926.....	Wetumka, Hughes Co., Okla.	7	
<i>R. foliolosa</i> alba (d) 9526, Ralph Shreve, 1926.....	Montagu Co., Texas	7	
<i>R. subserrulata</i> (a) (d) 9528, Ralph Shreve, 1926.....	W. Fork, White River, Okla.	7	
<i>R. rugosa</i> (hyb.) $\times$? <i>blanda</i> ($\times$ <i>R.</i> <i>tetonkaha</i>) (b) (d) 5328, N. E. Hansen, 1925.....	Hort., Brookings, S.D.	7	
TRIPLOID TYPES			
(?) <i>R. virginiana</i> $\times$ <i>palustris</i> (a) (b) (d) (e) (f) (g) 2872, E. C. Rob- bins, 1922.....	Highlands, Macon Co., N.C.	71171	21
(?) <i>R. blanda</i> $\times$ <i>carolina</i> (a) (b) (d) (e) (f) (g) 2949, W. E. Manning.	Esty's Glen, Ithaca, N.Y.	71171	21

TABLE II—Continued

SPECIES, ACCESSION NO., AND ORIGINAL COLLECTOR	ORIGIN	HAP- LOID NO.	SO- MATIC NO.
TETRAPLOID TYPES			
<i>Pacific Coast Cinnamomeae</i>			
R. californica (d) (e) (g) 5849, W. A. Archer, 1924.....	Toulomne River, Modesto, Calif.	14	
R. aldersonii (b) (d) (g) 5367, C. C. Epling, 1925.....	Griffith Park, Los Angeles, Calif.	14	
R. brachycarpa (a) (d) (g) 5301, H. Baer, 1924.....	Temescal Canyon, Elsinore, Calif.	14	
R. myriantha (a) (d) (g) 3537, Ellen Bach, 1923.....	Nevada City, Nevada Co., Calif.	14	28
<i>Carolinae</i>			
R. virginiana (d) (g) 2790, M. Bilon, 1922.....	Madison, New Haven Co., Conn.	14	
R. virginiana (d) (e) 6071, P. F. Weatherill, 1924.....	Orr's Island, Cumberland Co., Me.	14	
R. virginiana (b) (d) (g) 3236 (plant C) Hort.....	Naperville Nurs., Naperville, Ill.	14	
R. obovata (e) (g) (h) 2651, E. W. Erlanson, 1922.....	Ann Arbor, Washtenaw Co., Mich.	14	
R. deamii (d) (e) (g) 3779, C. C. Deam, 1923.....	Goldsmith, Tipton Co., Ind.	14	
R. lyoni (e) 2883, C. C. Deam, 1923	St. For. Res., Clark Co., Ind.	14	
R. lyoni (e) 3168, L. F. Brumfield, 1923.....	A. & M. College, Oktibbeha Co., Miss.	14	
R. lyoni (b) (e) (g) 3203, J. T. Buchholz, 1923.....	Fayetteville, Washington Co., Ark.	14	
R. carolina L. (d) (g) 5808, H. H. Bartlett, 1924.....	Camp Custer, Kalamazoo Co., Mich.	14	
R. carolina L. (g) 5291, David Boot, 1924.....	Iowa City, Johnson Co., Iowa	14	
R. carolina var. litoralis (e) 2654, A. H. W. Povah, 1922.....	Evanston, Cook Co., Ill.	14	
R. serrulata Raf. (d) (e) (g) 5566 (plant A), F. K. Sparrow, 1923.	Montgomery Co., Md.	14	
R. serrulata Raf. (e) 3938, Bartlett & F. C. Blanchard, 1923.....	Lakeland, Livingston Co., Mich.		28
R. subserrulata (a) (d) (e) 6072, W. A. Archer, 1924.....	Rogers, Benton Co., Ark.	14	
R. petiolata (d) (e) 3669, L. E. Wehmeyer, 1923.....	Boss, Dent Co., Mo.	14	
R. rudiusscula (a) (d) (e) (f) (g) 3501, E. W. Erlanson, 1923....	St. Charles, Kane Co., Ill.	14	
R. rudiusscula (a) (e) (g) 4001, C. C. Deam, 1923.....	Crown Point, Lake Co., Ind.	14	28
R. rudiusscula (e) 4293, B. F. Bush, 1923.....	Greenwood, Jackson Co., Mo.	14	
<i>Cinnamomeae</i>			
R. bushii Rydb. (d) (e) (g) 3080, B. F. Bush, 1923.....	Courtney, Jackson Co., Mo.	14	
R. alcea (h) 3571, S. Dowding, 1923	Calgary, Alberta	14	

TABLE II—Continued

SPECIES, ACCESSION NO., AND ORIGINAL COLLECTOR	ORIGIN	HAP- LOID NO.	SO- MATIC NO.
<i>R. subglauc</i> (a) (d) (e) 3492, A. H. Brinkman, 1923.....	Craigmyle, Alberta	14	28
<i>R. suffulta</i> (a) (b) (d) (e) (g) 2682, E. S. Reynolds, 1922.....	Agric. Coll., Cass. Co., N.D.	14	
<i>R. suffulta</i> (d) (e) (g) 2692, H. Stegenger, 1922.....	University, Grand Forks Co., N.D.	14	
<i>R. suffulta</i> (d) (e) 2694, H. Stegenger, 1922.....	University, Grand Forks Co., N.D.	14	
<i>R. suffulta</i> (a) (e) (g) 5598, U.S. For. Service, 1924.....	Monument, El Paso Co., Colo.	14	
<i>R. suffulta</i> (a) (d) (e) (g) 5615, W. A. Archer, 1924.....	Larkspur, Douglas Co., Colo.	14	
<i>R. suffulta</i> (g) 5705, E. V. Ander- son, 1924.....	Concord, Dixon Co., Neb.	14	
<i>R. suffulta</i> (d) 2897b, H. S. Con- ard, 1922.....	Grinnell, Poweshiek Co., Iowa	14	
<i>R. suffulta</i> (d) (e) (g) 3001, F. C. Gates, 1923.....	Riley Co., Kans.	14	
<i>R. suffulta</i> var. <i>valida</i> (a) (d) (e) (g) 4459, A. and P. Hamilton, 1923.....	Rockport, Atchison Co., Mo.	14	
<i>R. arkansana</i> 5771 (plant G) C. G. Harrold, 1924.....	Winnipeg, Manitoba	14	
<i>R. ratonensis</i> (b) (e) (g) 8114, C. O. Erlanson, 1925.....	Colfax Co., Raton Pass, N.M. (alt. 8800 ft.)	14	
<i>R. relict</i> a (g) 8320, C. & E. Erlan- son, 1925.....	Bliss Woods, Kane Co., Ill.	14	
HEXAPLOID TYPES			
<i>R. nutkana</i> Presl. 4004, C. C. Ep- ling, 1923.....	Priest River, Idaho	21	
<i>R. maddougali</i> (d) (e) E. 8, Arn. Arb. 12352.....	Idaho	21	
<i>R. spaldingii</i> 5549, A. A. Griffin, 1924.....	Naches River, Yakima Co., Wash.	21	
<i>R. spaldingii</i> 5298, A. A. Griffin, 1924.....	Tieton River, Yakima Co., Wash.	21	
<i>R. spaldingii</i> E. 4, Arn. Arb. 11116	Pullman, Whitman Co., Wash.	21	
<i>R. spaldingii</i> E. 7, Arn. Arb. 1268.	Idaho	21	
<i>R. spaldingii</i> E. 10, Arn. Arb.....	Elk Mt., Idaho Co., Idaho	21	
<i>R. engelmanni</i> 3254 (plant D), C. C. Moore, 1923.....	Missoula, Missoula Co., Mont.	21	
<i>R. engelmanni</i> , B. B. Kanouse, 1923			
3719 (e).....		21	
3721/A.....	{ Medicine Bow Mts., Albany Co., Wyo.	21	
3722 (e) (b).....		21	
3723.....		21	

TABLE II—*Continued*

SPECIES, ACCESSION NO., AND ORIGINAL COLLECTOR	ORIGIN	HAP- LOID NO.	SO- MATIC NO.
<i>R. engelmanni</i> (e) E. 5, Arn. Arb. 9052 A. Rehder, 1916.....	Pikes Peak, El Paso Co., Colo. (alt. 9000 ft.)	21	
<i>R. butleri</i> Rydb. (a) (e) 8271, C. O. Erlanson, 1925.....	Sangre de Cristo Mts., Custer Co., Colo. (alt. 8400 ft.)	21	
<i>R. underwoodii</i> Rydb. 8270, C. O. Erlanson, 1925.....	San Isabel Nat. For., Custer Co., Colo. (alt. 8400 ft.)	21	
<i>R. acicularis</i> var. <i>lacorum</i> 6008, E. W. Erlanson, 1924.....	Prentis Bay, Mackinac Co., Mich.	21	
<i>R. acicularis</i> var. <i>rotunda</i> 3511, C. O. Erlanson, 1923.....	Douglas Lake, Cheboygan Co., Mich.	21	
<i>R. acicularis</i> var. <i>bourgeauiana</i> (b) (e) (g) 2592, H. H. Bartlett. ...	Mackinaw City, Cheboygan Co., Mich.	21	
<i>R. acicularis</i> var. <i>sayiana</i> , J. H. Ehlers, 1922 (a) (b) (d) (e) (f) 3754 (plant A), 3754 (plant D).	Prentis Bay, Mackinac Co., Mich.	21	
<i>R. acicularis</i> var. <i>sayiana</i> 6007, C. & E. Erlanson, 1924.....	Scotty Bay, Mackinac Co., Mich.	21	
<i>R. acicularis</i> Lindl. E. 3 Arn. Arb., 789-5.....	Hort, Kew	21	
<i>R. acicularis</i> var. <i>nipponensis</i> (d) E. 14, Arn. Arb., 7839.....	Hort. Chénault, France	7	
OCTOPOLOID TYPE			
<i>R. acicularis</i> var. <i>lacorum</i> 6447, C. H. Morgan, 1924.....	Fairbanks, Alaska	28	

sometimes reaches over 7 feet in height. Morphologically it is the most highly evolved of the *Carolinae-Cinnamomeae* east of the Rocky Mountains. In northern Michigan and Wisconsin it has early-flowering races. These are also diploid, and were first recognized by SCHUETTE. Some of these seem to be due to hybridization between *R. blanda* Ait. and *R. palustris*, and are taxonomically distinct. Three of them have already been described as *R. michiganensis*, *R. schuetteana*,³ and *R. blanda* var. *hermanni* (ERLANSO

³ *Rosa schuetteana* resembles *R. carolina* L. in some respects, and was at first reported as that species (18). Cytologically it exhibits few irregularities, and has less than 10 per cent of sterile pollen. Since the tetraploid *R. carolina* has not been found in Cheboygan County, Michigan, it seems more probable that this species is descended from *R. palustris* × *R. blanda*, both of which are diploid forms, instead of from *R. carolina* × *palustris*. The flowering time of *R. schuetteana* is intermediate between those of *R. blanda* and *R. palustris*. This is one case in which cytological examination has aided in the classification of a rose form.

19). These plants exhibit a few irregularities in meiosis, chiefly due to lagging chromosomes during the first and second anaphases. There is a certain amount of polyspory, but the proportion of dwarf pollen grains is small, no larger than in the two hypothetical parents.

HURST (31) thinks that there are five primary groups of diploid species in *Rosa*, which he designates as AA, BB, CC, DD, and EE, each with a distinct set of linked factors. In his report before the Genetical Society at Cambridge, England (32), he designated *R. palustris* as tetraploid AADD and *R. blanda* as diploid DD. *R. palustris*, however, is undoubtedly a diploid species and is typically very distinct from *R. blanda*. These two species would be expected to belong to different primary groups.

DIPLOID SPECIES OF CINNAMOMEAE

A semidouble form of *Rosa cinnamomea* found growing wild in New York proved to be diploid. This record is of interest owing to the conflicting chromosome counts which have been obtained for this species. HURST (32) reported that there exist tetraploid varieties of this species which are "quadrivalent in synapsis."

TÄCKHOLM's findings as to the diploid nature of *R. pisocarpa* A. Gray⁴ (fig. 3), *R. woodsii* Lindl. (fig. 4), and the closely related *R. fendleri* Crép. and *R. macounii* Greene have been confirmed in wild material. Other species from the Rocky Mountain region, related to these, which have been found to be diploid, are *R. ultramontana* S. Wats., *R. salicetorum* Rydb.⁵ (fig. 5), *R. pyrifera* Rydb., and *R. puberulenta* Rydb. These are all tall roses and are characteristic of the waterways. So far as I know, the largest wild roses in any region in this country are the diploid forms, the polyploid forms being as a rule low shrubs growing to 4 feet in height, but usually under 3 feet high in nature.

Rosa granulifera Rydb. and *R. hypoleuca* Woot. & Stand., both

⁴ Specimens of *R. pisocarpa* in most herbaria are of two distinct types: (a) true *R. pisocarpa* with straight ascending infrastipular prickles, oval leaflets, and small hips in crowded corymbs; (b) plants with more scattered weak armature or none, more narrowly oval or obovate leaflets with triangular coarser teeth, larger flowers and hips. These latter belong to the *R. macounii* complex.

⁵ This specific name was misspelled in the original publication as *R. salictorum* (RYDBERG 48).

closely related to *R. fendleri*, are diploid as would be expected (figs. 6, 7).

In the group of *R. woodsii*, reduction takes place in the pollen mother cells when the buds are very small, about 2 mm. in diameter by 5 or 6 mm. long. In the following diploid forms the buds are large, about 4.5 mm. in diameter and 8 mm. or so long, when pollen formation takes place.

As already determined by PENLAND (46), *R. blanda* is a regularly diploid species. I have not been able to find any form of this species showing twenty-eight somatic chromosomes, and do not think that TÄCKHOLM's tetraploid specimens belonged to this species. They may have been some of the forms near *R. bushii* Rydb. and *R. rudiuscula* Greene. ALMQUIST determined them as *R. acicularis*.

Rosa subblanda Rydb., a glabrous relative of *R. blanda*, is diploid, as are all the forms of *R. blanda* which have been examined (fig. 8). There are numerous bristly types of *R. blanda*, corresponding to *R. blanda* var. *hispida* Farwell, which are found in widely separated parts of the range of the species, and nearly all exhibit some irregularities during meiosis. The most frequent irregularities are the failure of one or two pairs of chromosomes to be included in the first spindle (fig. 9), or the lagging of some pairs at first anaphase. Rarely at the second division a small extra spindle is observed. Some chromosomes may lag at this division also, and become inclosed in subsidiary nuclei giving polypspory. It is not usual to find more than one extra grain from a pollen mother cell, and counts of mature pollen reveal an appreciable and variable proportion of shriveled grains, from 6 to 33 per cent. These bristly varieties of *R. blanda* when collected in the western parts of its range are usually named *R. macounii*. *R. macounii* is probably a composite species, consisting in part of pubescent varieties of *R. woodsii* (most botanists so interpret *R. macounii*), and in part of more robust forms which should be placed in *R. blanda* var. *hispida*.

R. acicularioides belongs in the group of *R. blanda*, and there are cytological indications that it is of hybrid origin. A specimen from New York was found to be diploid, but some of the chromosomes show a weak affinity at meiosis and in some cells may fail to pair at all. Fig. 20 shows a first meta-anaphase in which four of the chromo-

somes have apparently failed to pair, the members of one pair lying at widely different depths on the spindle. The daughter nuclei will each receive seven chromosomes, however, and several sister interkinesis nuclei have been found, each one of which contains seven chromosomes and a nucleolus. Somatic cells show fourteen chromosomes (fig. 21). The plant from which the fixations were made produces abundant fruit, although castrated buds do not develop. If, under HURST's scheme, it contains two similar differential septets of chromosomes, let us say DD, one would expect to get complete pairing between the seven homologous pairs; if on the contrary it contains two different septets, say C and D, it should be sterile under this scheme.

DIPLOID HYBRIDS

R. blanda glandulosa Schuette

A culture of over 200 seedlings grown from seed of four separate plants of *R. blanda* var. *glandulosa* Schuette is growing at the University of Michigan Botanical Garden. The parent plants were collected in Mackinac County, Michigan, by Dr. J. H. EHLERS in 1923 (accession no. 3753), and the seeds of each were planted separately when they were received from the field. The seeds germinated in 6 months and throughout the first season the seedlings were fairly uniform. These plants came to maturity in 1926 and by then showed great variety. The stems now vary from almost unarmed to densely bristly throughout; in color they vary from red-brown to greenish brown. The hips vary from long-pyriform to globose, and may be either erect or pendulous when ripe. Several of the plants have glandular-compound teeth on the leaflets, as in *R. acicularioides* Schuette. Several plants did not flower in 1926, their third year of growth, and a few of these still failed to produce flowers in 1927. About half a dozen plants were badly cut back by the winter of 1925-1926, in spite of the fact that the parent plants came from latitude 46° north. The majority of the seedlings flowered profusely in 1926 and 1927, at the same time as *R. blanda*, and produced a full crop of large hips full of good achenes. *R. blanda* var. *glandulosa* is characterized by having pyriform hips, and has been called *R. acicularis* × *blanda* by RYDBERG (48). The morphology of the culture

just described would seem to confirm this diagnosis. Table III analyzes the progeny of the four plants for some characteristics often used to distinguish species in *Rosa*. The majority of the plants bear ellipsoid hips, although these may vary from subglobose to ellipsoid on the same plant. As a rule those individuals which have gland-compound teeth do not have them exclusively; those exhibiting any have been placed in the category "gland-compound." During the

TABLE III

VARIATION IN PROGENY OF FIELD-POLLINATED ROSES

Numbers of specimens exhibiting certain characteristics in cultures grown from seeds of four individual plants of *Rosa blanda* var. *glandulosa* Schuette (no. 3753), from Mackinac County, Michigan; seeds taken from parent plants when received from the field in 1923

CULTURE AND TOTAL NUMBER OF PLANTS	CHARACTERISTICS								
	Semi- hardy	No flowers in 1926 only	No flowers in 1926 or 1927	Leaflet teeth		Hip shape		Sepals	
				Simple	Gland- com- pound	Sub- glo- bose	Ellip- soid	Glan- dular	Smooth
3753/2 (50 offspring)	3	11	4	41	9	11	32	29	14
3753/5 (34 offspring)	0	10	3	32	2				
3753/7* (Total progeny 133, data taken on 75) . .	14 in 133	15	16	67	8	32	12	32	13
3753/9 (16 offspring)	0	1	1	7	9	1	10	8	1

* The progeny of 3753 plant 7 contained five plants that bore few flowers and no fruit in 1927, two plants that bore only one deformed hip in 1927; plant N54 had glabrate leaflets and several of the hypanthia aborted after anthesis.

first season the seedlings all had glabrous leaflets with glandular-compound teeth, two characteristics which seem to be universal among *Rosa* seedlings, although in some species the leaflets may become eglandular after the first two or three leaves are produced. In the seedling plants of no. 3753, some show glandular-compound teeth only on the leaves at the tips of turions and vigorous lateral shoots, toward the end of the season. In habit and flowering time most of these plants are like *R. blanda*. They also possess the corymbose inflorescence of that species. A few plants show partial sterility, in that only a few hips are produced and these contain only three or four achenes. One plant (9/N5) flowered but produced no fruit in 1927. Only one plant in the whole culture (7/N117) flowered

appreciably before the rest and showed habit and foliage typical of *R. acicularis*.

Thus far one of the parent plants and nine of the seedlings have been examined cytologically and all but two have been found to be diploids with fourteen somatic chromosomes (fig. 10). Pollen counts made on two of the apparently fertile plants showed 17.6 and 25 per cent of dwarf shriveled grains. The fact that the fixed material of culture 3753 exhibits a great deal of shrinkage, distortion, and chromatin extrusion strengthens my belief that it is of hybrid origin. (CLAUSEN [9] found that the distortion caused by fixation was particularly troublesome in his hybrid *Violae*.) At diakinesis there is a marked delay in pairing among some of the chromosomes (figs. 11, 12), some of which may still be unpaired at the time of heterotypic metaphase. The metaphase plates of the second meiotic division have been found showing seven chromosomes in both daughter nuclei. Some polyspory is evident, as would be expected from the condition of the pollen.

Two of the semihardy plants, which produce no flowers and have only a weak vegetative growth, were brought into the greenhouse, and root tips were fixed in Flemming's fluid, half strong. These showed fourteen somatic chromosomes (fig. 13).

Individual with fifteen chromosomes

Only two of the plants so far examined (culture 3753, plants 9/N1 and 7/N37) showed any extra chromosomes. One of these (plant 9/N1), a plant with glandular-compound teeth, has fifteen somatic chromosomes (fig. 14). At diakinesis there may be more than one univalent chromosome; fig. 15 shows three. There is some lagging at both meiotic divisions. The seven bivalent chromosomes and one univalent may lie on the first spindle (fig. 16), or some may not be included in it. Fig. 17 shows three pairs off in the cytoplasm. Interkinesis nuclei show both seven and eight chromosomes; in fifty cells thirty-five contained seven and fifteen eight. Fig. 18 shows two daughter nuclei at second metaphase. The extra chromosome has already divided and may have done so at first anaphase. In fig. 19 both the daughter nuclei show seven chromosomes at second metaphase, and the extra chromosome has apparently been extruded

and lies on the surface of the shrunken protoplast. This plant then probably produces gametes, mostly with seven, but occasionally with eight, chromosomes. It is a vigorous bush over 4 feet high and bore large crops of tapering hips in 1926 and in 1927.

R. blanda × *acicularis*

The plants of culture 3753 apparently are a later generation, perhaps many times removed, from a cross between the diploid *R. blanda* and the hexaploid *R. acicularis* of northern Michigan. Such a cross would be expected to give seven bivalents and fourteen univalent chromosomes at reduction division of the first hybrid generation. These hybrids would be expected to be highly sterile, only those gametes receiving few or no univalent chromosomes being able to function. It is possible that the elimination of the univalents through lagging on the spindles at meiosis led to the establishment of the largely stable and fertile diploid type resembling the diploid parent. Such reestablishment of constant types in later generations from crosses between individuals with different chromosome numbers has been found to occur in *Triticum* (KIHARA 38), in *Oenothera* (BOEDIJN 6), in *Papaver* (by a back cross to one of the parent types) (YASUI 67), and has been suggested by HEILBORN (29) as the way in which *Draba magellanica* with twenty-four chromosomes originated.

The great variation in the culture and the presence of some plants with glandular leaflets and pendulous pyriform hips (characters absent in *R. blanda*) suggest affinities with *R. acicularis*, and seem to show that in the original cross seven chromosomes from each parent paired, as would be required by HURST's scheme; but according to that scheme the progeny of such a cross would be sterile. There are in this culture, from four wild unguarded plants, forms that would be named *R. blanda*, *R. blanda* var. *glandulosa*, *R. blanda* var. *hispida*, and *R. acicularioides*, as well as sterile forms.

During the summers of 1926 and 1927 the cross *R. blanda* × *R. acicularis* and its reciprocal were successfully produced several times. The former cross yields as good a crop of achenes as any cross I have made. *R. woodsii* crossed with hexaploid types has also given good fruit. It may be significant that crosses between diploid and poly-

ploid roses are more often successful when the diploid is the female parent. Attempts to germinate these seeds have so far yielded only one seedling, but there is every indication that these crosses occur and are successful in nature.

It seems highly probable that some of the North American diploid roses have arisen in the manner suggested from crosses between some other diploid with a polyploid form. Such an origin would complicate matters, and would be more in accord with the taxonomic confusion proverbial in this genus than an origin of diploids from polyploids, according to HURST's theory, by the simple loss of sets of seven chromosomes. The variability of the diploid descendants of such crosses is likely to be great, and they can be expected to cross with each other and with the parent forms in the field, to continue to segregate and to give fresh combinations.

The first generation offspring of crosses between parents with different chromosome numbers are probably few and highly sterile, hence inconspicuous in the field. The flowering times of our hexaploid, diploid, and tetraploid roses are characteristic and often distinct, and wide crosses are presumably infrequent in nature. However, the possibility of the production of strong fertile descendants from such crosses in two or three generations permits the taxonomist to ascribe to hybridization the many intermediate forms so notorious in *Rosa* throughout the world.

R. acicularis var. *nipponensis* Koehne.

It is pertinent to record here that two plants from two different cultures of *R. acicularis* var. *nipponensis* growing at the Arnold Arboretum have been examined cytologically. One is diploid with seven pairs at diakinesis, producing good fruit; the other is almost sterile, seldom producing fruit and the fixed material is very badly shrunken, having seven pairs and also some univalent chromosomes at diakinesis. The plants were grown from seed sent by CHÉNAULT from France. Material that TÄCKHOLM obtained from Kew as this variety he found to be tetraploid. The seeds of *R. acicularis* var. *nipponensis* were distributed to the botanical gardens of Europe by the Hortus Petropolitanus about 1870 (WILLMOTT 65). It may be that since then the plants have crossed with others having different

chromosome numbers, until finally a fertile diploid form has been obtained in the same manner that the stable diploid seems to have been produced from *R. acicularis* × *blanda* in Michigan.

R. rugosa hyb. × *blanda* (?)

The Tetonkaha rose originated by HANSEN (26), supposedly from the foregoing cross, is diploid, as would be expected from a cross between two diploid species. HURST (32) has reported this cross, and according to his scheme it is CC × DD and should be sterile, unless it became fertile by a somatic duplication, thereby becoming tetraploid CCDD. The Tetonkaha rose produces large hips resembling those of *R. rugosa*, and apparently crosses with other roses, since seed obtained from another plant growing at Washington, D.C. gave large seedlings with the habit of *R. multiflora* or *R. arvensis*. These latter, however, do not set fruit. Apparently crosses between very distinct diploid species may give fertile offspring.

MEIOTIC IRREGULARITIES IN DIPLOIDS

The early history of meiosis in all the species examined has corresponded with that described by BLACKBURN and HARRISON (4) for *R. arvensis*. The chromosomes are arranged end to end, and sometimes pairing is considerably delayed after strepsinema during condensation, so that strings of chromosomes appear (fig. 5). Frequently the members of some pairs become attached by their ends alone, thus forming a ring (fig. 12), these configurations recalling similar ones in *Oenothera*. Frequently two chromosomes in a nucleus will delay pairing until the first spindle is formed. In some cases, although all the chromosomes may come to lie on the equator of the first spindle, the members of one pair may fail to associate with each other (fig. 20). It is noticeable that condensation proceeds irregularly among the chromosomes after fragmentation of the spireme, so that it is not unusual to find the majority of the pairs well condensed, with one or two still long and threadlike. This state of affairs is also true among the tetraploids (fig. 38 A).

Meiosis in North American diploid roses is seldom completely regular as it was found to be in *R. arvensis* by BLACKBURN and HARRISON. Most of the forms studied resemble cytologically the

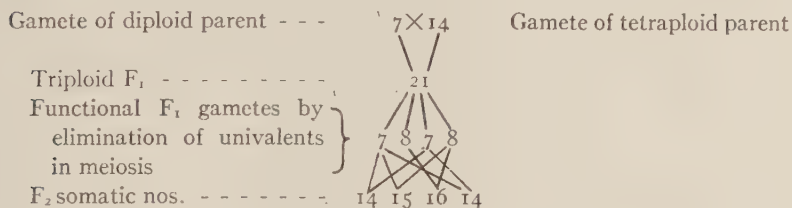
diploid hybrids examined by TÄCKHOLM. Sometimes one or more pairs of chromosomes fail to reach the first spindle (figs. 9, 17), and may lag behind the others at first anaphase. The interkinesis nuclei usually receive seven chromosomes, but there may be more lagging at second anaphase. These irregularities are reflected in the presence of polypory (fig. 24) and in the pollen counts (table IV), which show a considerable proportion of shriveled grains for species in which PENLAND considers hybridization scarcely to exist.

Extrusion of chromosomes, upon which HURST lays so much stress, is frequent in all stages of meiosis, and is more noticeable in the more sterile plants than in others. In how far this phenomenon is an artifact is not yet known; my material seems to show that in many cases it is probably due to imperfect fixations. Fig. 6 shows two contiguous cells in which extrusion at diakinesis is commencing; the nuclear membrane in both cells has been drawn out nearer to the edge of the protoplast and has been broken through in the same relative position, which suggests a too sudden penetration of the fixing fluid from one side. The number of chromosomes extruded may vary, as found by LONGLEY (41) in triploid *Rubus* species. Occasionally all the chromosomes of many cells in a loculus are found to be extruded, or more rarely all the chromosomes of a cell are extruded into the cytoplasm of a neighboring pollen mother cell (fig. 15). Even according to HURST's theory there does not seem to be further need for extrusion once the plants have become diploid.

TYPES WITH SIXTEEN CHROMOSOMES

A small culture of plants (no. 6610) grown from seed sent by Mr. A. O. GARRETT from Utah, from a plant identified at the United States National Herbarium as *R. pyrifera* Rydb., exhibits a considerable amount of variation. All have glabrous leaflets as in *R. woodsii*. One plant has sepals that are erect on the fruit; another has sepals that are spreading or reflexed, with small lateral pinnae. The fruit of the latter resembles that of *R. californica*, and it also ripens later than that of the former plant. In 1927 very few flowers were produced, and, unfortunately, buds from two plants were fixed together. Cytological examination revealed that one plant is a regular diploid while the other has an extra pair of smaller chromo-

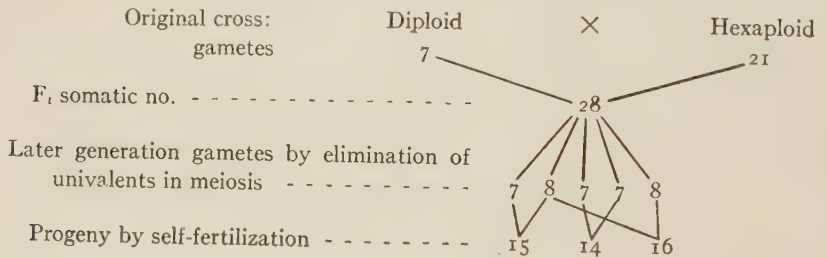
somes, giving eight pairs at diakinesis (figs. 22, 23). The bud with sixteen chromosomes also exhibits a phenomenon pertaining to nuclear disturbance which is absent in the diploid bud; that is, meiosis does not take place synchronously. Scattered in a single anther loculus some tetrads of young pollen grains can be found, as well as sporocytes undergoing reduction division and also some at diakinesis. This condition was noticed in the pollen sacs in the perfect flowers of *Populus tremuloides* (ERLANSON and HERMANN 20); it is said by TÄCKHOLM (59) to characterize hybrid forms of *Rosa*. It is probable that the plants from Utah are descendants from a cross involving a diploid (perhaps *R. woodsii*) and some polyploid form (perhaps a tetraploid). In our culture 3753 a plant with fifteen chromosomes (plant 9/N1) and one with sixteen chromosomes (see later) have been discovered. All these aneuploid forms may have been produced from viable gametes that possessed eight instead of seven chromosomes. A hybrid plant with fifteen chromosomes might produce several gametes with eight chromosomes, and by self-fertilization give rise to offspring with sixteen chromosomes. It would also produce gametes with seven chromosomes and could therefore give progeny with fourteen and fifteen chromosomes, as shown in the following diagram:



It is significant that one of the pairs at diakinesis in the bud of *R. pyrifera* with sixteen chromosomes is smaller than the others. CLAUSEN (9) reports that in *Viola* hybrids in which the unpaired chromosomes divide at both meiotic divisions, the chromosomes that result are smaller than the others in the next generation.

Material fixed from plant no. 7/N37 in culture 3753 of *R. blanda glandulosa* showed no reduction stages in the microsporocytes. In one ovule, however, four young megaspores were found each showing eight chromosomes (fig. 25). The chalazal megaspore in the row is

already shrunken as if about to disintegrate; the two nearest the micropylar region are side by side instead of being in linear order, but one is larger than the other. TÄCKHOLM (59), and earlier STRASBURGER (57), found that in *Rosa* the micropylar megaspore is the functional one. Somatic counts of this plant show clearly sixteen chromosomes (fig. 26). It is conceivable that the plants of culture 3753, showing as they do fourteen, fifteen, and sixteen chromosomes, all arose from a fertile hybrid ancestor with fifteen chromosomes, suggested diagrammatically as follows:



Aneuploid forms are rare in *Rosa*. TÄCKHOLM only found five among 293 individuals; I found three among 108.

TRIPLOID TYPES

Among over 100 individuals which have been examined cytologically from the collection at Michigan, only two (and a possible third) have been found to be triploid, possessing twenty-one somatic chromosomes.

R. palustris × *carolina*, no. 2872

Specimens received from North Carolina as *R. lucida* (syn. *R. virginiana*) are vigorous and form a dense thicket. The stems are over 3 feet high, greenish brown, and weakly armed; they bear many flowers in small corymbs and begin to bloom in the second or third week of June at Ann Arbor. After anthesis all the hypanthia usually shrivel and fall off. Very rarely one or two small hips are formed, each containing only one or two achenes. The hypanthium in flower is glabrous; the pedicels bear a few stipitate hispid glands; the achenes are basally attached; and the sepals remain reflexed or spreading on the occasional hips.

A great deal of shrinkage and distortion due to fixation gave

similar effects to those noticed by CLAUSEN in his *Viola* hybrids, and impeded cytological examination. At diakinesis in the microsporocytes seven paired and seven unpaired chromosomes appear (fig. 27), the latter being noticeably small. All these elements become grouped on the equator at the first meiotic metaphase (fig. 28), and one member of each pair passes to each pole. The univalents become scattered along the spindle, and usually pass as whole chromosomes to the poles, being distributed at random. There is a tendency for the univalents to become fragmented at this stage, although this may be due to the fixing fluid. A similar effect was observed by GATES and THOMAS (25) in pollen mother cells of *Oenothera lutea*, which is also a highly sterile form due to the presence of an extra unpaired chromosome. Lagging, unpaired chromosomes occasionally divide at the equator in the first anaphase; but only rarely, since, in the few sister interkinesis nuclei observed, in no case did the sum of their chromosomes total more than twenty-one. At late interkinesis and second metaphase varying numbers of chromosomes (usually 8–12) were found. The material does not show many cells in this stage, and only one case was observed in which the daughter nuclei contained either seven or fourteen chromosomes. Fig. 29 shows sister second metaphase plates with nine and twelve chromosomes respectively. Since no chromosomes are visible scattered in the cytoplasm, it is to be concluded that the unpaired seven passed whole to the poles, two going to one and five to the other. The second meiotic division exhibits several irregularities; extra spindles with two or three chromosomes are not infrequent. On the main spindles all the chromosomes usually begin to split and to separate simultaneously, but during anaphase some of the halves lag behind and fail to become included in the major grand-daughter nuclei. Apparently some of the chromosomes may fail to split at second anaphase and instead pass whole to the poles. Fig. 30 shows a second meta-anaphase spindle on which the seven large chromosomes (originally conjugants) have divided or are in the process of dividing; of the seven smaller chromosomes (originally univalents) three are dividing at the equator, one lies partly split at one pole, and the other three seem to be passing entire to the poles, two to one and one to the other. If all the chromosomes reach the poles,

the two resulting microspores will receive twelve chromosomes each, but in an entirely irregular manner. Polyspory is much in evidence. There are a few tetrads of pollen grains but usually from five to ten cells result from one sporocyte (fig. 31). In some microsporangia a few sporocytes fail to undergo meiosis, and can be observed full of fat globules, apparently breaking down among young microspores. Other sporocytes may give rise to two pollen grains only, and these may both be approximately of the same size and both large (fig. 32); rarely one member of a diad is almost twice the size of the other. It has not been possible to observe whether such diads are the result of a microsporocyte failing to develop beyond the first meiotic telophase, or whether at second telophase the chromosomes become included in two nuclei as observed by BLACKBURN and HARRISON (4) in *R. sabini*.

Culture 2872 is thus seen to be a good example of the "*Drosera*-type" of meiosis, and therefore resembles in its cytological behavior four of the five triploids whose meioses were observed by TÄCKHOLM. This type of meiosis is interpreted as being due to the fact that all the members of a smaller gametic chromosomal complement pair with members of a larger gametic complement, in the sporocytes of hybrids from a cross between two parents having different chromosome numbers. It is further characterized by TÄCKHOLM as having all the unpaired chromosomes irregularly distributed as whole chromosomes to the poles at first anaphase. It was originally observed by ROSENBERG (47) in his *Drosera rotundifolia* $\times$ *longifolia* hybrid, and since then in hybrids of *Morus* by OSAWA (45), of *Triticum* (SAX 51, 52), of *Fragaria* (ICHIJIMA 33), and of other plant genera. Complete accounts are given by TÄCKHOLM (59), SHARP (55), and MORGAN (44).

Since these *Rosa* plants came from North Carolina and their cytology reveals them to be offspring from a cross between a diploid ($x=7$) and a tetraploid ($x=14$), it is not difficult to assign putative parents. The only diploid species of the Cinnamoneae-Carolinae in the region is *Rosa palustris* Marsh., the tetraploid species being *R. carolina* L. and its varieties (or closely related and doubtfully distinct species), and possibly *R. virginiana* Mill. The triploid plants form dense thickets like those of *R. palustris*, although the habit is

more slender and weedy. The leaves are narrow and lance-elliptic, with finer teeth than in *R. carolina* and its allies, or than in *R. virginiana*. It flowers with the two latter species, two weeks or more before *R. palustris*. The occurrence of true *R. virginiana* in this region is doubtful, so that it is highly probable that these plants are hybrid *R. palustris* × *carolina*, the *R. humilis gracilis* of Porter MS according to RYDBERG (49). Our plants have weak, straight, infrastipular pickles or none, and the stems are bristly at the base. The fact that the hypanthia are glabrous is not significant, since the characteristic hispid glands are not infrequently absent from some individuals in both *R. palustris* and *R. carolina*.

Pollen examination revealed very little pollen in a flower bud, and of what was produced not a single grain was observed which was plump and yellow; all the grains were transparent and wrinkled, 60 per cent of them being misshapen and the pollen 100 per cent bad. In examining ovules from these plants no stages of meiosis have been observed, nor any embryo sacs. Some tetrads of megaspores have been seen, and in some cases all four spores appeared to be disintegrating. In one case the megaspore nearest the micropyle was still large while the other three were shrunken.

Culture 5590 (?) R. palustris × *virginiana*.—In a small culture of *R. palustris* grown from seeds sent by Dr. H. M. DENSLOW from New Jersey, six seedlings out of nineteen were noticed to have gland-compound teeth during the first season. In the following year (1926) all had simple teeth. They flowered for the first time in 1927, one plant beginning to bloom 8–10 days before the others. Unfortunately it was not observed until it was almost past flowering, and buds fixed then showed neither meiosis nor mitosis. However, a great deal of shriveled pollen was evident, and a count of mature pollen showed only 3 per cent of good grains. After flowering all the hypanthia shriveled and fell. In one bud 88 stamens were counted, about 100 less than the usual number in *R. palustris*. The plant is low in stature and the leaflets are distinctly ovate with coarse teeth; the other plants in the culture are typical of *R. palustris*. This sterile plant is therefore suspected of being a triploid hybrid, perhaps *R. palustris* × *virginiana*. This case emphasizes the necessity for growing large cultures of wild roses in order that the sterile and often

weak hybrid forms with interesting chromosome complements may appear, as well as to give an adequate idea of variation. It is often very difficult to obtain cultures because of slow and poor germination.

Culture 2949 (?) R. blanda $\times$ *carolina*.—The second plant which has been demonstrated cytologically to be a triploid with twenty-one somatic chromosomes was sent from Ithaca, N.Y., by Mr. W. E. MANNING. It is a low weak plant about 18 inches high, and produces very little vegetative growth. It is almost unarmed, possessing only a few weak paired infrastipular prickles. The leaflets, usually seven, are glabrous and glaucous, or have a few hairs on the veins beneath. The teeth are fine and ovate, smaller than is usual in *R. blanda* or *R. carolina*. It flowers toward the end of June, at the same time as *R. carolina*, bearing solitary flowers on the old wood but small terminal corymbs on some of the season's turions. Subglobose hips about 1 cm. in diameter are set. These and the pedicels are entirely glabrous. After anthesis the sepals are reflexed or spreading but are persistent. The achenes are basally attached, as is usual in *R. carolina* and occasional in *R. blanda*. The stamens vary from 140 to 155 per flower, about as in *R. carolina*; in fact, the plant strongly resembles some forms of *R. carolina* which are almost unarmed and eglandular.

At diakinesis in the microsporocytes of this triploid plant some cells show seven pairs of conjugating chromosomes, although fewer usually appear (fig. 33), and in a few cells the affinity is so weak that all twenty-one appear as distinct units, although some are grouped together in pairs they are not closely appressed. There is some extrusion of chromosomes at this stage, but so far as observed the number that pass from one cell into the next is variable, from one or two to all the chromosomes.

At early first metaphase all the bivalent and univalent members become grouped somewhat irregularly on the equator, the members of the pairs beginning immediately to disjoin and pass to opposite poles. The univalents split and seven half chromosomes often pass to each pole after the seven whole ones (fig. 34). There does not seem to be any definite grouping of the univalents and bivalents on the first metaphase plate, as is the case in many of the Caninae; in

fact, it is usual for some of the chromosomes to lie at various levels on the spindle, giving an irregular effect. Some of the univalents seem to have difficulty in dividing, so that the chromatic material becomes drawn out along the spindle fiber between the two halves. In some cells a few of the univalents fail to split, passing to one of the poles entire at first anaphase. In one such cell observed, nine chromosomes could be counted at one pole while four univalents were to be found dividing at the equatorial region; in another there were also nine chromosomes at one pole and five univalents were dividing at the equator. The distribution of chromosomes in 100 second metaphase plates was counted, and is shown as follows:

No. of chromosomes.	7	8	9	10	11	12	13	14
No. of plates.	1	4	14	23	15	13	12	18

The following distribution was observed in seventeen pairs of sister second metaphase plates. One pair had 14 and 13 chromosomes respectively; one had 14 and 12; two had 14 and 10; one had 14 and 9; one had 14 and 8; one had 14 and 7; one had 13 and 13; three had 13 and 12; two had 13 and 9; one had 12 and 11; one had 12 and 10; one had 11 and 10; and one had 10 and 10. In only five cases out of these seventeen does the sum of the chromosomes in two sister nuclei amount to only twenty-one or less, which might mean that in those cells none of the univalents had divided at first anaphase, providing all the chromosomes reached the poles. If all the univalents divided at first anaphase the daughter nuclei should each receive fourteen chromosomes. The two factors which prevent the sums of the chromosomes of sister nuclei from being twenty-eight are: first, all the univalents do not divide in every cell at first anaphase; second, all the split univalents are not included in the daughter nuclei. Nevertheless 30 per cent of these receive thirteen or fourteen chromosomes (fig. 35), and only in one case were sister plates observed containing seven and fourteen chromosomes respectively.

The second anaphase is usually initiated very regularly, all the chromosomes lying in one plane on the equator and all beginning to split simultaneously, in contrast with the conditions found in 2872. By the time second telophase is reached, however, some of the

chromosomes may lag behind the rest and fail to reach the poles. Many of the microsporocytes give rise to tetrads of microspores, and, although polyspory is frequent there are seldom more than two or three subsidiary spores produced. Examination of the pollen showed more shriveled grains than was expected, only 7.3 per cent of large plump grains being found in over 400 counted.

This plant (2949) resembles cytologically the triploid *R. centifolia major* examined by TÄCKHOLM (as no. 194), and the percentage of good pollen is very little more than that found in *R. centifolia major* by HURST (30). This type of meiosis has been called the "*Rosa*-type" by TÄCKHOLM, who first found it fully developed in the microsporocytes of the Caninae wherein all the unpaired chromosomes split at first meiotic anaphase. Our triploid from New York approaches very nearly to the *Rosa* type of meiosis, since it appears that nearly all the unpaired chromosomes divide at both meiotic divisions. The triploid from North Carolina, on the other hand, behaves almost as ROSENBERG's *Drosera* hybrids, only rarely any of the unpaired chromosomes dividing at first anaphase.

Possible occurrence of fertile triploids

The outstanding point of interest about the New York triploid type is the fact that it produces a crop of good hips and achenes. As all students of *Rosa* know, the cytological examination of meiosis in the megasporocyte is difficult. Since our plants are small it has been possible to fix only a few buds; flowers have been needed for herbarium vouchers and also for seed. In ovules of accession no. 2949 good normal embryo sacs have been seen, as well as one case of two ovules in one carpel and a case of two embryo sacs in one nucellus. Such abnormalities have been observed before in the genus (STRASBURGER, TÄCKHOLM), and are considered by some to be characteristic of hybrids (JEFFREY 35, 36). No stages of meiosis have yet been discovered in the ovule, and three castrated flowers gave no fruit. In the absence of direct evidence as to chromosomal behavior during megasporogenesis, there are two alternate possibilities to be considered as explanations for the fertility of this plant.

As a first alternative the plant may resemble the Caninae, in which case all the unpaired chromosomes in the megasporocyte pass

as a group to one pole at first meiotic anaphase, and the daughter nucleus receiving fourteen chromosomes gives rise to the functional megaspore. If, as in the Caninae, only those pollen grains containing seven chromosomes are functional, there would be only a small chance for this plant ever to produce zygotes by self-pollination, if one judges from the distribution of chromosomes in second meiotic metaphase nuclei. By the time second telophase is reached some grand-daughter nuclei may receive only seven chromosomes, due to lagging during the second anaphase, as is the case in the Caninae. Should the specimen correspond in this way to the roses of the Caninae, it would thereby give rise to a freely fruiting triploid race of North American roses, either by apomixis or by the fusion of a fourteen-chromosomed egg with a seven-chromosomed sperm nucleus. The extreme rarity of triploids in my material, and the fact that none have been reported by others from this continent, would seem to preclude this possibility, although our plant might be the starting point for such a line. Such triploids, strongly resembling tetraploid types, as does our plant, and setting fruit freely, would be very difficult to recognize as hybrids in the field unless one examined the pollen.

The second alternative is that meiotic behavior in the ovules of this plant corresponds to the process in the microsporocytes, as is the case in other Cinnamomeae. If this were so we could expect an appreciable number of both megaspores and microspores to receive fourteen chromosomes, and there would be produced a zygotic tetraploid form with twenty-eight chromosomes from a triploid parent by self-pollination. The plant would then resemble CLAUSEN's *Viola* hybrid, in which the somatic number in the F_2 generation was increased over that in the F_1 by a double splitting of unpaired chromosomes during meiosis. KARPECHENKO (37) also found that this took place in some *Brassica* $\times$ *Raphanus* hybrids. The increased chromosome number observed by BREMER (8) in a hybrid from a species cross in *Saccharum* may have come about in this way. The possibility that our plant may produce some spores that receive only seven chromosomes is not ruled out.

In the central United States there are many *Rosa* forms which are very puzzling taxonomically. Some of them appear to be inter-

mediate between *R. suffulta* (tetraploid) and *R. blanda* (diploid), for example, *R. relict*a Erlanson. It may be that these actually originated from crosses between diploid *R. blanda* and tetraploid forms, and that the resulting triploid hybrids were fertile as is 2949, giving rise to fertile tetraploids or perhaps to some diploids in the following manner:



According to HURST's theory of differential septets, if the two parents were respectively CC and CCDD, there would be the re-establishment of the tetraploid parent type by the duplication of the unpaired D chromosomes in the F₁ hybrid. To a certain extent this is true, since the rose forms in question have many characteristics of other tetraploids, yet they are distinct from *R. suffulta* and exhibit some characteristics of *R. blanda*.

The tetraploid *R. damascena* is known to have given rise to a triploid form in cultivation, and HURST (31) believes this to be due to the loss of a septet by extrusion. Since our fertile triploid strongly resembles *R. carolina*, it might be attributed to a loss of seven chromosomes in one of the parent gametes, but the idea of its possible hybrid origin seems to be more in conformity with known proceedings in other organisms.

In 1927 six field-pollinated hips were collected from 2949, containing 13, 8, 6, 5, and 4 achenes respectively. Out of three buds which were self-pollinated, one contained only two achenes and the other none. Too much emphasis must not be laid on the apparent failure of self-pollination, since it has been found very difficult to obtain seeds in this way from many of the North American *Rosa* species, particularly in *R. blanda*. It may be that bagging the whole inflorescence causes the pollen to become damp and non-functional, or there is the possibility of some self-sterility. FOCKE (23) gives *R. blanda* × *lucida* as a garden hybrid.

Infrequency of triploid roses

The fact that I have been able to find so few triploid roses is surprising, especially considering the great number of triploid forms LONGLEY (41, 42) found in *Rubus* and *Crataegus*. One reason for this no doubt is the fact that our tetraploid and diploid species of *Rosa* are so often separated both in space and in time of flowering. In the eastern part of the continent *R. blanda* (diploid) flowers before *R. virginiana*, *R. carolina*, and their allies (tetraploids), while *R. palustris* (diploid) comes into flower last of all. In the western part *R. woodsii* and its allies (diploid) flower before *R. suffulta* (tetraploid) and before *R. californica* (tetraploid). Also, the diploid forms are characteristic of waterways and swamps, while the tetraploids are usually found on dry uplands and plains. Further extensive field work will no doubt bring to light other hybrids between the two groups, and crosses already have been successfully made experimentally.

TETRAPLOID TYPES

There are two very distinct groups of tetraploid rose species in North America, widely separated geographically. These are the *R. californica* group on the Pacific Coast, and the large group comprising *R. virginiana*, *R. carolina*, and *R. arkansana* and their allies. The former two are distributed over the eastern half of the continent north to the Great Lakes and the St. Lawrence, and the latter is characteristic of the great plains of the Mississippi drainage system.

R. californica and allied species.—TÄCKHOLM (59) found *R. californica* to be diploid with seven pairs at diakinesis. I have examined one individual of this species and one of each of the closely related species *R. brachycarpa* Rydb. and *R. aldersonii* Greene, which are perhaps only varieties of *R. californica*. All three show fourteen pairs of chromosomes at reduction division in the pollen mother cells (figs. 38-40). The allied species *R. myriantha* Carr, obtained from Nevada City, which morphologically is somewhat intermediate between *R. californica* and *R. pisocarpa*, is also tetraploid (fig. 41).

Middle-western and eastern species.—Cytological examination has confirmed TÄCKHOLM's findings that *R. virginiana* Mill., *R. carolina* L. (*R. humilis* Mill.), and *R. suffulta* Greene all have twenty-eight somatic chromosomes and fourteen pairs at reduction division.

This group of roses is extremely variable and difficult taxonomically. In addition to the usual morphological variations, this group shows marked geographical and local races which present great difficulties to descriptive definition. It has long been a moot point whether *R. carolina* is a variety of *R. virginiana* or not because of the intergrading series of forms found between the two in the northeastern United States (BEST 2). In the middle western region there is an equally notable intergrading series of forms between *R. carolina* and its varieties and the *R. arkansana-suffulta* group, giving forms like *R. rudiuscula* Greene and *R. conjuncta* Rydb.

Tetraploid and diploid races of R. subserrulata Rydb.—When a specimen from Oklahoma, which agrees morphologically with *R. subserrulata* Rydb., was examined cytologically, it was very unexpectedly found to be diploid, showing seven chromosomes at first and second metaphases with only a slight amount of lagging during meiosis, and an occasional chromosome off in the cytoplasm. Another specimen belonging to this species, from Arkansas, was examined and found to be tetraploid, as would be expected from its close resemblance to *R. carolina*. The tetraploid plant (no. 6072) shows several irregularities during meiosis. At first anaphase from three to five pairs may lag behind the others; fig. 59 shows three lagging pairs as well as two unpaired chromosomes, one of which is beginning to divide. Early first telophases usually show fourteen chromosomes (fig. 61), and in one case two distinct groups of seven chromosomes were found at this stage (fig. 60). Except for this example, which could be due to chance grouping, I have not seen any evidence for chromosomes separating in groups of seven at reduction division as HURST's theory would seem to demand, if the septets, which he regards as linkage groups, are to remain intact. According to HURST's theory the diploid *R. subserrulata* might be regarded as having been produced from a tetraploid form by loss of a diploid set of septets. The origin of both the diploid and tetraploid types of *R. subserrulata* can also be postulated from a fertile triploid producing functional gametes with both seven and fourteen chromosomes, as suggested under the New York specimen 2949.

This case of *R. subserrulata* is one of only two in which have been found different chromosome numbers in two individuals apparently

belonging to the same species. The diploid *R. subserrulata* was received from Mr. RALPH SHREVE late in 1926, and flowered in the cold frame in 1927. At present I do not know whether it produces flowering turions or not. The common widespread glandular form of *R. carolina*, *R. serrulata* Raf. (*R. carolina* var. *glandulosa* Farwell), was found to have twenty-eight somatic chromosomes in a Michigan specimen (fig. 47) and fourteen pairs at diakinesis in a specimen from Maryland (no. 5566, plant A).

Meiosis in megasporocyte.—The diad stage of meiosis was observed in an ovule of a plant from Aurora, Illinois (no. 3501) which I consider to be a form of *R. rudiuscula* Greene (fig. 62). One of the cells is in interkinesis while the other is entering second metaphase. Both show fourteen split chromosomes.

MEIOTIC IRREGULARITIES IN TETRAPLOIDS

Early stages of meiosis in the tetraploid forms resemble similar stages in the diploid types. The chromosomes are attached end to end, and each usually becomes paired with one adjoining individual. Condensation of the chromosomes is irregular. Fig. 38 shows a diakinesis nucleus in *R. californica* in which there are twelve pairs, a ring of three and one long, unpaired chromosome. Rings of four chromosomes are often present during diakinesis, but they usually break up into two pairs by the time the first meiotic metaphase is reached, and well condensed groups of four are not as common as are rings (figs. 42, 52). There is most frequently only one ring of four to a nucleus, although two or even three have been observed (fig. 51). Fig. 46 shows a cut cell at early first anaphase in which a ring of four chromosomes has not yet succeeded in condensing and reaching the spindle.

In some nuclei at diakinesis there seems to be a tendency for half of the chromosomes to pair intimately quite early, while the other fourteen lie adjacent to each other in pairs but seem to have a decidedly weaker affinity. This is particularly noticeable in species of the *R. suffulta* complex (figs. 49, 53). Some of the members of this group sometimes possess certain characteristics of *R. blanda*, and are often associated with it in the field; and, as has been suggested, may have arisen as a cross between that species and some

tetraploid. The discovery of the fertile triploid 2949, which could conceivably give rise to a fertile race of tetraploids by self-pollination, suggests a possible origin for such anomalous tetraploid forms. One would expect that chromosomes which were originally halves of a single individual would pair very intimately at diakinesis.

In some cases a few of the chromosomes in a tetraploid microsporocyte fail to pair at all at diakinesis, and, just as among some diploids, they appear on the first metaphase spindle as univalents (fig. 56). During first anaphase there is nearly always some lagging of one or two pairs, but each pole usually receives fourteen (figs. 40, 43). It is also evident that occasionally some of the chromosomes that fail to pair will divide at late first anaphase (figs. 54, 57, 59). This was observed by TÄCKHOLM in his tetraploid specimen no. 132, which was named *R. blanda*, as well as in some of his tetraploid hybrids. Second anaphase may be regular (fig. 50), or there may be some lagging and extra nuclei at second telophase (fig. 58).

Cytologically nearly every tetraploid specimen examined showed meiotic irregularities which differ only in degree from those found in known tetraploid hybrids examined by TÄCKHOLM. A dwarf plant of *R. subglauca* Rydb. from Alberta (no. 3492) shows many such irregularities. At first meiotic metaphase nearly all the chromosomes lie loosely associated in pairs (fig. 55) or some fail to pair. Fig. 56 shows four univalents on the spindle. Some of them split at first anaphase (fig. 57), and there is some lagging so that all do not reach the poles. Fig. 58 shows a sporocyte at second telophase in which one pair of grand-daughter nuclei contain fourteen chromosomes each; the other pair twelve and thirteen respectively. Five extra chromosomes and two split ones lie in various positions about the cell, making a possibility of nine chromosomes not included in the four nuclei. Since this makes a total of sixty-two chromosomes instead of a normal fifty-six, three univalents have divided at both metaphases.

Polyspory is more frequent among tetraploids (fig. 48) than among diploids, and the percentage of bad pollen is larger on the average (table IV). Extrusion is frequent, as in the diploids, and the number of chromosomes thus lost seems to be arbitrary.

POSSIBLE ORIGIN OF TETRAPLOID TYPES

One of the most striking characteristics of meiosis in the tetraploids is the presence of groups and rings of four (instead of two) chromosomes at diakinesis. This is shown in several of the figures. TÄCKHOLM does not seem to have observed it. It is frequent in my material and resembles the configurations found in tetraploid *Datura* plants by BELLING and BLAKESLEE (1), although in no case has a cell been observed that is completely quadrivalent in synapsis. The tetraploid condition may have arisen in these forms by duplication from the diploid, and have become modified in later generations by crossing-over, non-disjunction, and hybridization, until a single individual only possesses one to three quadrivalent sets of homologous chromosomes. Tetraploid roses may have arisen more than once on this continent by duplication in more or less sterile diploid hybrids. This is known to have occurred in the case of *Primula kewensis* (DIGBY 17), in *Nicotiana* (CLAUSEN and GOOD-SPEED 10), in *Raphanus* × *Brassica* hybrids (KARPECHENKO 37), and in *Rosa wilsoni* (HARRISON and BLACKBURN 5). WINGE (66) believes that lack of harmony between chromosomes from two parents, even when their numbers are the same, may lead to reduplication, giving tetraploids from hybrid diploids. From his work on *Viola*, CLAUSEN (9) concludes that such doubling is important in biological evolution, and will produce "biologically stable types." Duplication, on the other hand, which produces true tetraploidy with quadrivalent sets of homologous chromosomes, he believes to be of little consequence in phylogeny, such types being unstable and likely to revert to the original diploid state.

The possibility that a tetraploid form with all the chromosomes pairing might be produced from a cross between a diploid and a hexaploid among the Cinnamomeae should not be entirely overlooked, even though this would involve pairing between the chromosomes from one parent, a condition that has not been observed in *Rosa*. LONGLEY (43) found that in a cross between *Vaccinium corymbosum* (haploid number of 24) and *V. virgatum* (with $x=36$), the F_1 hybrid occasionally showed as many as thirty pairs at diakinesis, although the hybrid was highly sterile.

MORPHOLOGICAL CHARACTERISTICS AND DISTRIBUTION
OF TETRAPLOIDS

It soon became noticeable among our living collection that nearly all the North American tetraploid species are characterized by the ability to produce flowers terminally in corymbs on the season's turions, a behavior peculiarly adapted to a prairie habitat where the aerial stems are likely to be frozen down in winter and burned off by fire in summer. They are also characterized by their long flowering period, some of them continuing to bloom after ripe fruit is developed, a performance never observed in any of the other native groups, although exhibited by *R. rugosa* Thunb. *R. acicularis*, however, will occasionally have a second blooming late in a mild autumn.

I had hoped that the ability to flower on the season's turions would prove to be a criterion for tetraploidy in American roses, and for the most part this is true. In *R. virginiana*, the largest of the eastern tetraploid species, this ability is only weakly developed and some plants will not produce flowering turions every year. It is very common in *R. californica*. *R. ratonensis* Erlanson in some ways resembles *R. woodsii*, but can immediately be distinguished from that species by its strong turions bearing terminal corymbs. It is a tetraploid.

The most unexpected exception to this generalization was the discovery of a diploid specimen of *R. subserrulata*, a possible hybrid origin of which has been previously considered.

Another exception to this character being confined to tetraploids is *R. foliolosa* Nutt., a diploid species of the Carolinae from Texas and Oklahoma. This is a low semi-herbaceous species that bears very little wood over 2 years old. It flowers in small corymbs, terminally on the annual shoots. If this species originated as a haploid from a tetraploid form and still retained the tetraploid "ever-blooming" characteristic, it would from its southern distribution be an argument in support of HURST's theory of the loss of extra septets of chromosomes from polyploids in southern habitats. It is a very distinct species, its narrow numerous leaflets and small (sometimes curved) prickles resembling, if anything, diploid *R. palustris*, whose western limit is well to the east of the range of *R. foliolosa* (text fig. 1), rather than any form of tetraploid *R. carolina*.

Our collection does not contain any mature *R. nitida* Willd. This species was reported as diploid by TÄCKHOLM, and it may also possess the ability to flower on the season's turions, although this is not mentioned in descriptions and can seldom be discovered from herbarium specimens. It will be of interest to discover whether the other dwarf species, *R. gamella* Willd. and *R. nanella* Rydb., also Carolinae with limited ranges in the northeastern Atlantic region, are diploid or tetraploid. *R. relictæ* Erlanson, a dwarf form from Illinois, and the low growing *R. bushii* Rydb. are both tetraploid. The third exception is the case of a dwarf plant from Calgary, Alberta (no. 3571). After three years in the garden it is little more than a foot high, a small branched woody bush resembling in habit the specimen of *R. subglaucæ* from Alberta (no. 3492). The former plant agrees with the description of *R. alcea* Greene. It grows very slowly and has produced no turions. The dwarf *R. subglaucæ* has produced one or two flowering turions. Both these specimens are tetraploid.

With the exception of *R. virginiana*, in the northeast, and of *R. californica*, the North American tetraploid roses are of low stature, usually under a meter. The tetraploid species belonging to the section Cinnamomeae are more specialized in habit and inflorescence type than the related diploid forms, and are perhaps of more recent origin. The setaceous stems and numerous leaflets are considered by BOULENGER (7) as relatively primitive characteristics in *Rosa*, but they almost always appear on young turions, and would be expected on plants with a semiherbaceous habit. Some of these forms, more particularly *R. suffulta* and its allies in the Mississippi region, have a markedly semiherbaceous habit, which appearing in a frutescent group is generally considered a more highly evolved condition (SINNOTT and BAILEY 56). BEWS (3) points out that the stream bank and swamp habitat is one of the primitive unchanging habitats of angiosperms, and that the grassland habitat is a relatively recent one; hence he maintains that plants adapted to the latter are derived and not primitive forms. As already stated, the North American diploid roses are characteristic of waterways (as are the hexaploids), while the tetraploids belong to the prairies and dry uplands.

From every point of view the tetraploid forms seem to be more

highly evolved and of more recent origin than any other form in the group of Cinnamomeae-Carolinae in America.

Among the tetraploid Carolinae, *R. virginiana* stands out as the most robust and fruticose type. This species seems to be confined to the northeastern Atlantic region, although a whole series of forms can be found between it and the typical low weedy *R. carolina*, as well as between this latter species and the tetraploid Cinnamomeae of the *R. suffulta* complex. All these types flower almost synchronously when grown together. The significance of this will be considered in the discussion of phenology in *Rosa*. The tetraploid Carolinae have a very extensive north and south range, from the St. Lawrence to northern Mexico. It is noticeable that the glandular types of the *R. carolina* complex preponderate in the southern part of its range; this is also true for the western diploid *R. woodsii* complex, which has an even greater north and south range than the Carolinae, stretching from British Columbia to Chihuahua.

HEXAPLOID TYPES

All North American forms of *R. acicularis* examined, except one individual from Alaska, showed twenty-one pairs of chromosomes at metaphase at the first meiotic division in the microsporocytes (fig. 63). This species is typically boreal and alpine, and SCHNEIDER (54) was without doubt in error in attributing a Texan specimen to it. Specimens collected in the Sangre de Cristo Mountains of southern Colorado by C. O. ERLANSON grew at altitudes between 8000 and 13,000 feet; they are hexaploid and agree with RYDBERG's descriptions for *R. butleri* and *R. underwoodii* (fig. 64). After having examined several thousand herbarium specimens of North American roses, I have seen no specimens belonging to the *R. acicularis* complex from farther south than the mountains of southern Colorado.

As has been found by others, *R. nutkana* Presl. is also hexaploid, as are the allied species *R. spaldingii* Crép. (fig. 65) and *R. macdougalii* Holz. *R. engelmannii* S. Wats., which is somewhat intermediate between *R. acicularis* var. *sayiana* and *R. nutkana* in the northern Rockies, is also hexaploid. The hexaploid forms exhibit very few irregularities in meiosis. Both divisions are usually almost schematic in regularity. Extrusion occurs (fig. 64); delayed pairing at di-

akinesis and lagging chromosomes have only been observed in one or two cases; polyspory is rare (fig. 66); and pollen examination reveals a very low percentage of poor pollen, in all cases less than 10 and often under 5 per cent.⁶

The *R. acicularis* forms are the first of the American species to flower in the spring, and the pollen mother cells are frequently damaged by frost at the end of May. They are followed in about a week by *R. nutkana* and its allies. In all these species the buds are relatively large (8–10 mm. long) when pollen formation takes place. Although these forms show few cytological disturbances, it is evident from the variations in cultures that they hybridize freely among themselves. Neither is artificial hybridization between hexaploid forms difficult. The hexaploids are not larger plants than the diploid *Cinnamomeae*.

Just as in the region of the Great Lakes, botanists have always found difficulty in distinguishing some forms of *R. blanda* from *R. acicularis*; so in the Rocky Mountain region there are many forms intermediate between *R. nutkana* and *R. acicularis*. In the case of the two latter species the flowering times are more nearly approximate, and the chromosome complements of the two species are alike, thus making chances for successful crossing greater. I suspect that *R. engelmanni* is a product of such a cross, and hope to produce it artificially in the garden. Hexaploid species have been crossed successfully to diploid forms. Crossing tetraploids with hexaploids has not been attempted, for, although their ranges overlap in the eastern foothills of the Rocky Mountains and in the northern great plains region, the wide difference in time of flowering between the two groups almost precludes this cross in the field.

As HARRISON and BLACKBURN (27) have pointed out, the hexaploid condition probably arose from the union of a tetraploid with a diploid gamete followed by duplication in a triploid hybrid. The greatest concentration of hexaploid types on this continent seems to be in the northern Rocky Mountain region, and their distribution is continuous in all directions from thence. No hexaploids have been

⁶ I wish to express my thanks to Dr. REHDER and Mr. JACK for extending to me the privilege of collecting cytological and herbarium material from the interesting hexaploid roses in the Arnold Arboretum collection in 1926.

found outside the continuous range of *R. acicularis* in regions where diploid and tetraploid forms both occur; that is, in the northwestern part of the great plains, and in the United States east of the Mississippi (text figs. 1, 2); so that it would appear as though the hexaploid type has not arisen more than once, if at all on the American continent. There has not been discovered a hexaploid in the section *Carolinae*. The hexaploid types of *Cinnamomeae* may have entered America from northeastern Asia and spread south and east over the continent.

Meiosis in ovule.—Meiosis has not been observed in the megasporocyte of any hexaploid type. Stages in fertilization as well as a normal two-celled embryo have been observed in *R. acicularis* var. *lacorum* from northern Michigan (text fig. 3). Castrated buds have continually failed to give any fruit.

R. nutkana and related species.—The diploid *R. pisocarpa* and the tetraploid *R. californica* both show some morphological resemblance to *R. nutkana*. This fact has been evident to students of the Pacific Coast roses. WATSON (63) placed *R. californica* and *R. pisocarpa* in the same subdivision. In determining TÄCKHOLM's material, ALMQUIST identified the diploid "*R. californica*" specimens from Lund and Kew as varieties of *R. nutkana*, and gave the same treatment to the *R. pisocarpa* specimens. It is fairly certain that former students of the Pacific Coast roses have usually had only small series of specimens at their disposal, and have misunderstood the species as did CRÉPIN (RYDBERG 48). Nevertheless there is a superficial morphological resemblance between these species in some respects, just as there is between *R. acicularis*, *R. blanda*, and *R. suffulta* in the northern great plains region, although one would never confuse them in a living collection. There is thus some evidence supporting the suggestion of HARRISON and BLACKBURN (27) that the North American *Cinnamomeae* species have a dual origin, one group of species arising from *R. nutkana*. Their "neat proof," however, from the presence of a specific rose gall insect is unfortunately not justified by the work of KINSEY (40) on which they base it.⁷ It has

⁷ Dr. KINSEY informed me that it was not his intention to affirm that *Diplolepis bassetti* is "confined to *R. nutkana*." The following are extracts from his letters in 1926: "The host record which I gave for *Diplolepis bassetti* should have been applied only to the type material of variety *bassetti*. . . . I have no determinations of any sort



FIG. 1.—Map showing distribution of Carolinac: area of diploid species delimited by dots; tetraploids by crosses

seemed to me for some time that the two series of species groups (1) *R. nutkana* (hexaploid), *R. pisocarpa* (diploid), *R. californica* (tetraploid), in the far west and (2) *R. acicularis* (*R. sayi*) (hexaploid), *R. blanda* (diploid), *R. suffulta* (tetraploid), or *R. acicularis*, *R.*



FIG. 2.—Map showing distribution of American Cinnamomeae: area of hexaploid species delimited by crosses; diploids by dots; tetraploids by wavy line.

woodsii, *R. arkansana* in the Mississippi region, are analogous in the origin and relationship of the contained forms. If the chromosome numbers in our species have become reduced in phylogeny, as HURST claims, this has apparently not been in a simple descending series, and there seems to be no reason to suppose that the process which

on the roses from which I secured additional material of the same variety. . . . The only material which I have shows nothing but a remnant of a stem without leaves. . . . I have no notion what rose this species (*Diplolepis bassetti*) occurs on and I am very much inclined to believe that it occurs on more than one rose in this wide range (i.e. Oregon, Idaho and Utah)."

produces forms related to the polyploid species but with smaller chromosome numbers is anything other than hybridization, followed by the loss of unpaired chromosomes, as previously suggested under diploid species.

OCTOPOLOID TYPE

A large bush of *R. acicularis* from Europe at the Arnold Arboretum, which was grown from seed sent from the Royal Gardens at Kew, has only twenty-one pairs at diakinesis, as found also by PEN-



FIG. 3.—Two-celled embryo of *R. acicularis* var. *lacorum* no. 6007 (hexaploid)

LAND (46), and not twenty-eight as in European material from Sweden and Russia examined by TÄCKHOLM.

An individual from a collection sent by Professor C. H. MORGAN from Fairbanks, Alaska (accession no. 6447) was found to be an octoploid with twenty-eight pairs at diakinesis (figs. 67, 68). Meiosis in this form is regular throughout and no polyspory has been observed. The plant possesses very glandular foliage and narrow pendant hips, and fits well into *R. acicularis* var. *lacorum* as described from the Great Lakes region (ERLANSON 18), differing from that form only in its earlier flowering period. Herbarium specimens of the European forms of *R. acicularis* were examined in the Crépín Herbarium at Brussels in 1925, and no distinguishing morphological character could be found, that would hold out in a series of speci-

mens, to distinguish them from North American types of the species. All that can be said is that glands on the foliage are far commoner in American than in European types, in which glands are exceptional. There does seem to be some difference in habit, however, the European bushes that I have seen in botanical gardens branching more freely and reaching a greater height than our specimens. The Alaskan plants in our collection thus far show no marked habit differences from the other American forms. This, therefore, is the second case in which two individuals have been discovered apparently belonging to the same species yet possessing different chromosome numbers (the other case is mentioned under the tetraploid *R. subserrulata*).

The octoploid *R. acicularis* has exceptionally few deformed pollen grains. In 400 grains examined not one shrunken and transparent grain was observed, the only irregularity exhibited in the pollen being 3.75 per cent of distorted and angular (though plump) grains amongst the normal ones.

Polyspory and apomixis

POLLEN EXAMINATION

The first published report of pollen examination in American rose species is that of CRÉPIN (15), who reports "pollen pur" in all the forms examined, except in the case of *R. californica*, the pollen of which he found "tantôt complètement pur, tantôt mélangé d'environ $\frac{1}{3}$ de grains atrophiés." He thought originally that the presence of dwarf grains gave "une précieuse indication dans le cas où une forme est soupçonnée d'hybridité," but was constrained to modify his views on account of the pollen sterility present in the Caninae. He found that the amount of bad pollen varied in different flowers from the same bush, and probably also from year to year. COLE (12) reported shriveled grains among the pollen of several American rose species but did not give actual counts. HARRISON and BLACKBURN (27) showed that the amount of bad pollen among roses of the Caninae varies from 10 to 100 per cent.

In order to examine pollen, anthers were taken from buds just before the petals opened, and stored over calcium chloride in a desiccator. The pollen was examined dry under the microscope and

the percentage of shriveled grains in a sample of about 500 was calculated. As shown in table IV, the octoploid *R. acicularis* and all

TABLE IV
PERCENTAGE OF STERILE GRAINS IN POLLEN OF AMERICAN ROSES

SPECIES	ACCESSION NO.	ORIGIN	PERCENTAGE STERILE POLLEN
<i>Diploid</i>			
<i>R. gymnocarpa</i>	4006	Idaho	9
<i>R. ultramontana</i>	5292	Washington	4.7
<i>R. salicetorum</i>	3530	Idaho	38.0
<i>R. woodsii</i>	5560	Montana	9.0
<i>R. fendleri</i>	2938	Colorado	25.6
<i>R. blanda</i>	2895	Iowa	10.0
<i>R. blanda</i>	3502	Illinois	52.0
<i>R. blanda</i> var. <i>hispida</i> . . .	2681	N. Dakota	4.3
<i>R. blanda</i> var. <i>hermanni</i> . .	2686	Michigan	6.0
<i>R. blanda</i> var. <i>glandulosa</i> .	3753/9	Michigan	17.6
<i>R. blanda</i> var. <i>glandulosa</i> .	5/N10	Michigan	25.0
<i>R. schuettea</i>	5891	Michigan	8.3
<i>R. michiganensis</i>	5890	Michigan	3.6
<i>R. palustris</i>	4412	Michigan	10.0
<i>R. palustris</i>	5714	Michigan	4.8
<i>R. palustris</i>	8626	Ohio	9.5
<i>Tetraploid</i>			
<i>R. californica</i>	5849	California	26.0
<i>R. aldersonii</i>	5367	California	22.0
<i>R. suffulta</i>	2682	N. Dakota	15.5
<i>R. suffulta</i>	3001	Kansas	29.0
<i>R. rudiuscula</i>	3501	Illinois	25.8
<i>R. bushii</i>	3080	Missouri	26.0
<i>R. relecta</i>	8320	Illinois	56.77
<i>R. carolina</i>	5716	Michigan	25.4
<i>R. carolina</i>	2946	New York	9.5
<i>R. virginiana</i>	6071	Maine	24.4
<i>R. virginiana</i>	4651	Connecticut	10.0
<i>Hexaploid</i>			
<i>R. spaldingii</i>	5298	Washington	8.0
<i>R. spaldingii</i>	5549	Washington	8.6
<i>R. butleri</i>	8271	Colorado	0.0 (8.3% angular grains)
<i>R. underwoodii</i>	8270	Colorado	8.3
<i>R. engelmanni</i>	3721	Wyoming	10.8
<i>R. acicularis</i> var. <i>lacorum</i> .	6008	Michigan	8.4
<i>Octoploid</i>			
<i>R. acicularis</i>	6447	Alaska	0.0 (3.6% angular grains)
<i>Triploid</i>			
<i>R. sp. indet.</i>	2872	N. Carolina	100.0
<i>R. sp. indet.</i>	5590	Connecticut	97.0
<i>R. sp. indet.</i>	2949	New York	92.7

hexaploid forms examined had about 10 per cent or less of shriveled pollen. Several diploid forms have less than 10 per cent of shriveled grains. *R. salicetorum* and *R. fendleri* showed 38 and 25.6 per cent

respectively. There is great variation in the amount of sterile pollen in different individuals of *R. blanda* and its varieties, varying from 4.3 to 52 per cent. Most of the tetraploids show from 15 to 25 per cent of bad pollen. Considerable difference is shown between two individuals of the same species in *R. carolina* and in *R. virginiana*. *R. relict*a Erlanson has the highest amount of sterile pollen of any form examined (except the triploids), one bud having 56 and another 77 per cent of bad pollen.

These counts demonstrate that many of our native rose species are partially sterile, a characteristic often associated with hybridity. It is very interesting to find that, among forms with all pairing chromosomes, the higher polyploids show the least amount of sterile pollen, while the tetraploids show the most; the diploids occupy an intermediate position in this respect, showing much variation.

CASTRATION EXPERIMENTS

TÄCKHOLM (59) has given an account of the castration experiments carried out in Europe on *Rosa*. HARRISON and BLACKBURN (27) report that several of the English Caninae are facultatively apomictical. HURST (30) reported the production of normal achenes after castration in *R. gallica* and other garden forms. Castration has been carried out on several North American species during the past three years, and in only two cases were fruits obtained subsequently. These were both in 1927 on plants of *R. blanda* from northeastern Illinois; plant 8321 on which two buds were castrated gave one small hip containing two achenes; six buds were castrated on plant no. 3502 and every one set a plump hip filled with achenes. In castrating, the androecium and the stigmas were removed with a razor blade but the buds were not bagged. The case of 8321 may have been due to a failure to remove all the stigmas; the case of 3502 is significant when its high percentage (52 per cent) of bad pollen is considered. ERNST (21) maintains that polyspory and apomixis are consequent upon hybridization.

Phenology in relation to phylogeny

Taxonomists formerly seem to have agreed that *R. acicularis* is the most primitive member of the Cinnamomeae (BOULENGER 7), and my observations tend to confirm this. The tetraploid forms

seem to be the most highly evolved and specialized of the American Cinnamomeae, while the related diploids are intermediate between the hexaploids and tetraploids. There appear to be two distinct series of hexaploid, diploid, and tetraploid forms, with ranges on the western and eastern sides of the Rocky Mountains respectively. In each series the hexaploids are boreal and alpine in distribution, the tetraploids temperate and southern (text fig. 2).⁸ In both of these series the diploids occupy a middle position in the southern part of the range of the series as a whole, and are intermediate in flowering time between the early-flowering hexaploid species and the later-flowering tetraploids.

There is some evidence that the phenological procession in the flora of the northern hemisphere, taken by and large, gives some clue to phylogenetic relationships, the vernal forms being the most primitive, as suggested by HARSHBERGER (28) and maintained by ILLITSCHEVSKY (34) at the International Congress of Botany in 1926 at Ithaca. This principle may also help in an understanding of the phylogeny of the species in some large boreal genera.

Phenological notes have been taken on the University of Michigan rose collection for three years, and each species complex is found to have a specific and characteristic flowering period. When taken in relation to each other each group of forms comes into flower in a definite order. In fact the "flowering time" of any individual is often a very good specific character, a fact to which CRÉPIN (14) first called attention. A collection of plants belonging to *R. blanda* var. *hispida* which was received from Manitoba (no. 5771) contained one plant which did not differ markedly from the others in habit, yet it began to bloom about 10 days later. Cytological examination revealed that the earlier blooming form was diploid while the latter one was tetraploid. Upon closer examination the latter specimen was found to have 7-9 glabrous leaflets; the petals were pale salmon

⁸ In text figs. 1, 2, and 4 the distribution areas have been plotted whenever possible from specimens seen by the writer. An "!" means that a specimen has been verified from that particular region. Doubt about the occurrence of a certain group is indicated by an "?" immediately following the number, which denotes the chromosome constitution of the group. The limits of the areas of distribution are approximately correct, although they may have to be extended in some directions when more specimens have been studied.

color, not rose pink as in the other plants; and the hips were larger with a slight neck. I have placed it under *R. arkansana* Porter. Although we have several collections of each species complex from different parts of its range, a hexaploid type from the mountains of Montana flowers synchronously with hexaploid forms from the mountains of southern Colorado and from central Michigan; even as tetraploid forms from North Dakota and Alberta bloom no earlier than those from Missouri. The many varieties of *R. blanda* obtained from stations all over its range all come into flower during the same week. The octoploid *R. acicularis* from Alaska is the first of the American plants to come into flower; in 1926 it bloomed a week before any of the hexaploid forms of this species.

Possible origin of polyploid series

CINNAMOMEAE

The conclusion that hybridization between many of our wild forms is general and of common occurrence in nature is supported by: (1) the successful production of good achenes by artificial crossing of different species with the same chromosome number, of diploids with hexaploids and of diploid with tetraploid forms; (2) the marked variation in the progeny obtained from seeds taken from individual wild plants in the field; (3) the large and variable percentage of sterile pollen present in many wild individuals; (4) the meiotic irregularities similar to those found by TÄCKHOLM in plants with a balanced number of chromosomes but which were known to be hybrids. Furthermore, it appears as though all crosses between parents with unlike chromosome number are not sterile. The evidence is strong for the theory of HARRISON and BLACKBURN of "the hybrid origin of orthoploid series in *Rosa* paralleling that in other plant genera." If this premise be accepted, it is possible to postulate an origin for the polyploid series which we find in the North American Cinnamomeae (table V). As COCKERELL (11) pointed out, the octoploid and hexaploid types were probably built up by duplication from primitive diploid roses, and although HURST does not mention this in his preliminary paper (31), this is also his idea of their origin.

The northern limit of hexaploid types on this continent is at present unknown, as is the southern limit of the octoploid *R. acicularis*. It is reasonable to suppose that both types reached America

TABLE V

Phylogenetic diagram

AMERICAN CINNAMOMEAE

Ancestral diploid forms by duplication and
hybridization → higher polyploids*R. acicularis* (octoploid) × *R. nutkana* (hexaploid)

↓ (or related form)

Heptaploid hybrid

↓
Later generations by elimination of univalent chromosomes↓
R. engelmanni, *R. acicularis sayiana*, *R. acicularis bourgeauiana*
(hexaploid types)*R. nutkana* (hexaploid) × (diploid) Generalized ancestral type of
↓ *R. woodsii* group

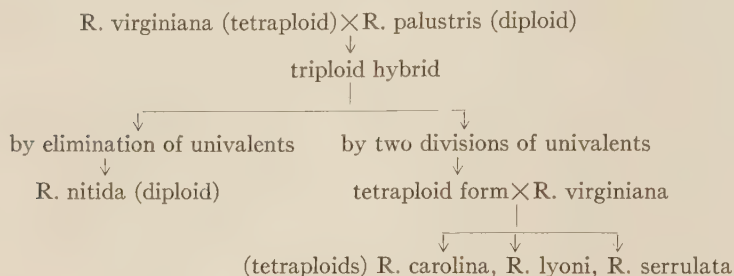
Tetraploid hybrid

7 bivalents and 14 univalents at diakinesis

↓
Later generations by elimination of univalents↓
R. pisocarpa (diploid) × diploid form↓
diploid hybrid↓
by duplication↓
R. californica (tetraploid)*R. acicularis sayiana* (hexa.) × *R. woodsii* ancestor (diploid)↓
Tetraploid hybrid↓
Later generations by elimination of univalents↓
R. blanda (dipl.) × *R. macounii*, *R. fendleri* (diploids)↓
diploid hybrid↓
by duplication↓
R. suffulta, *R. arkansana* (tetraploid) × *R. blanda*↓
triploid hybrid↓
by two divisions of univalents↓
R. relictata (tetraploid)

TABLE V—Continued

DIAGRAM OF POSSIBLE ORIGIN OF SOME CAROLINAE



from the northwest, coming from northeastern Asia, as suggested for the hexaploids by HARRISON and BLACKBURN (27).

In 1927, pollen from the octoploid *R. acicularis* was collected May 24 and kept in a desiccator until June 14; it was then used to pollinate four buds of *R. nutkana* from Idaho. Large hips were set, containing 16, 17, 22, and 22 achenes respectively. Seedlings from this cross would be expected to be heptaploid with forty-nine somatic chromosomes, and to show twenty-one pairs and seven univalent chromosomes at diakinesis. In F_2 and later generations a fertile hexaploid race might be reestablished by the loss of the unpaired chromosomes by lagging at meiosis, as has been found to occur in wheat hybrids (SAX 51, 52, 53; KIHARA 38, 39). These hexaploid descendants should possess some of the characteristics of each parent. Such a cross may well have been the origin of the American hexaploid forms such as *R. engelmanni*, *R. acicularis* var. *sayiana*, and *R. acicularis* var. *bourgeauiana*.

A good yield of achenes was obtained by crossing *R. woodsii* (diploid) with *R. spaldingii* (hexaploid), and also from crossing *R. salicetorum* (diploid) with *R. nutkana* (hexaploid). Some such cross, followed by an elimination of unpaired chromosomes in subsequent generations, may have given rise to the diploid *R. pisocarpa*. Some related sterile diploid form, by duplication, may have originated the tetraploid *R. californica*. Such a phylogeny does not seem too far-fetched, and would account for the resemblances already noted between *R. nutkana*, *R. pisocarpa*, and *R. californica*.

A hexaploid *R. acicularis* crossing with some member of the

diploid *R. woodsii* group, by elimination of unpaired chromosomes in later generations, could be imagined to have produced the *R. macounii-fendleri* group of diploid forms. Some one of these, crossing with *R. blanda* (or other diploid), may have resulted in a sterile diploid form, which by duplication gave rise to a fertile tetraploid race, the *R. suffulta-arkansana* group, which latter group of forms always seemed to CRÉPIN to be a variety of *R. blanda*.

The distribution map of the American Cinnamomeae (text fig. 2), although only approximate, brings out the fact that the diploid and hexaploid forms occur in that area of the continent which was occupied by the Pleistocene ice sheet (COLEMAN 13), the diploid forms having spread appreciably south of this area only in the western mountainous regions and in the foothills. The distribution area of *R. californica* lies well to the south of the glaciated area, and that of the tetraploid *R. arkansana* group is, for the most part, also to the south of it. The latter group is spreading rapidly both northward and eastward, however, having been found in the last few years both in southern Michigan and in northern New York.

The general area of distribution of *R. blanda* (text fig. 4) contrasts with that of the other Cinnamomeae in being northeastern and in not reaching the Rocky Mountains, although many closely related forms are found there. Whether *R. blanda* was already on this continent before the Pleistocene ice sheets advanced, and whether it therefore, upon their final withdrawal, advanced northward and westward, finally meeting the hexaploid and diploid forms coming in from the extreme northwest, is an interesting speculation.

CAROLINAE

The generalized distribution map of the Carolinae (text fig. 1) shows that these forms occupy the southeastern part of the continent, chiefly that region not occupied by the Cinnamomeae. In the case of the Carolinae, the diploid and tetraploid types occupy almost the same area, the tetraploids going farther into the southwest. The Cinnamomeae and Carolinae overlap chiefly in the Great Lakes region and in the central part of the Mississippi Valley, where tetraploid forms belonging to both sections are found. It is somewhat certain that these tetraploids hybridize and give rise to intermediate



FIG. 4.—Map showing distribution area of *Rosa blanda* Ait.

forms such as *R. rudiuscula* Greene, *R. bushii* Rydb., and *R. conjuncta* Rydb.

As stated elsewhere (ERLANSON 19), *R. palustris* and *R. blanda* appear to cross in the northern Lake Michigan region and to give stable forms. *R. virginiana* may be an ancient tetraploid type, and is typically limited to the northeastern Atlantic region. *R. palustris* crossed with *R. virginiana* would give a triploid hybrid, which would probably be sterile. Since no fertile hexaploid forms are known in this group, a fertile tetraploid may have been reestablished from such a sterile triploid by all the unpaired chromosomes dividing at both meiotic divisions, as in our accession no. 2949 from Ithaca, N.Y., and this tetraploid may have been the ancestral form of the complex of *R. carolina*, *R. lyoni*, *R. serrulata*. Specimens of *R. palustris* with gland-compound teeth have been observed in herbaria.

No sterile wild diploid type has yet been discovered, although there is the possibility that they exist and produce fruit apomictically.

The fact that vigorous forms, originally of hybrid origin, may spread beyond the distributional limit of at least one parent is seen in the case of *R. blanda* var. *glandulosa*, which is found farther south along the shores of Lake Michigan than *R. acicularis*. An alternate origin of the hexaploid forms on this continent from a cross between a tetraploid and diploid followed by duplication does not seem feasible from a consideration of the distribution data.

Hurst's theory of differential septets

Owing to the interest which HURST's theory of the origin of forms with lower numbers from higher polyploids in *Rosa* has aroused, the evidence for and against his interpretation, taken from findings in American material, follows.

Evidence favoring hypothesis

1. Octoploid *R. acicularis* is apparently arctic, with the hexaploid *R. acicularis* types boreal and alpine in distribution. The resemblance between the two types could be interpreted to mean that one "double septet" (fourteen homologous chromosomes) does not affect the octoploid plant and could therefore be dispensed with if eliminated by extrusion.

2. Two forms occur in southern stations, with flowering times and habit characteristic of tetraploids, yet having only fourteen chromosomes. These are *R. foliolosa* and the diploid *R. subserrulata*. The latter appears to be almost identical morphologically with the tetraploid *R. subserrulata*, and both it and *R. foliolosa* seem to be "haploid tetraploids" rather than simply primitive diploids. If this were so these forms could be interpreted as having arisen from tetraploid ancestors by the loss of half of the chromosomes ("one double septet") in southern latitudes.

Evidence against hypothesis

1. Neither HARRISON and BLACKBURN nor I have been able to discover any convincing cytological evidence for distribution of the chromosomes in sets of seven during reduction division in *Rosa*, as would be required by HURST's theory if the "differential septets" are to remain together as compound linkage groups. On the contrary, the cytology of many American forms demonstrates the independent and often irregular distribution of chromosomes at meiosis. In the same plant varying numbers of bivalent groups are present in different cells at first metaphase, and varying numbers of the univalents may be split at first anaphase. The fact that all gametes resulting from irregularities in meiosis, or containing extra chromosomes, are not sterile is shown by the existence of fertile, vigorous aneuploid plants.

2. Chromosome extrusion is frequently observed in the microsporocytes of *Rosa*, but the number of chromosomes thus lost from the cell seems to be arbitrary and variable, and is probably due to disturbances consequent upon hybridization.

3. It is very doubtful that all crosses between different "simple septet" species (diploids) give sterile diploid hybrids. Intermediate types between *R. palustris* and *R. blanda* (which are surely different "simple diploid species") in northern Michigan, such as *R. schuettea* and *R. michiganensis* (ERLANSOHN 19), have been found to be diploid and have very little sterile pollen.

4. If there are races within some species with different chromosome complements which are indistinguishable morphologically, as seems to be the case in *R. acicularis* and *R. subserrulata*, then we

cannot base a classification of the genus on the "numbers of somatic septets of chromosomes present in the species," as HURST proposes to do.

Summary

1. In this study 107 wild roses from known stations in North America were examined cytologically. The majority of the specimens fall into the three classes, diploid, tetraploid, and hexaploid, seven being the basic number. One specimen was octoploid, two were triploid, and three aneuploid with the somatic number not a multiple of seven.

2. Measurements show that the cells are larger in the polyploid forms.

3. The diploid American roses are robust plants, larger as a rule than the related polyploid species. Many of them exhibit irregularities during meiosis. In some individuals incomplete pairing at diakinesis, lagging chromosomes, and polyspory are frequent; these are believed to be spontaneous hybrids produced by the crossing of different species, or the descendants of such hybrids.

4. It is concluded that crossing occurs in the field between different diploid species in *Rosa*, giving rise to at least partially fertile diploid offspring.

5. Three fertile aneuploid plants, two with sixteen somatic chromosomes and one with fifteen, have been found among cultures of diploid plants. One such culture exhibits a great deal of variation and appears to be a later generation of a cross between the diploid *R. blanda* and the hexaploid *R. acicularis* of Michigan. Such a cross would give, in the first generation, tetraploid hybrids with seven pairs and fourteen unpaired chromosomes. During meiosis in these hybrids the unpaired chromosomes probably lag on the spindle, giving some fertile gametes with only seven or eight chromosomes, which by self-fertilization give rise to fertile diploid or aneuploid plants.

6. Two triploid plants have been examined cytologically. Both have seven paired and seven unpaired chromosomes at first reduction division. One exhibits the "*Drosera*-type" of meiosis and is sterile. The other has the "*Rosa*-type" of meiosis, in which the seven univalent chromosomes divide twice, making it possible for

some spores to receive fourteen chromosomes, although this is prevented in many cells by lagging on the spindle. This latter plant is not apomictical yet it sets good fruit. Reduction in the megasporocyte of the fertile triploid has not been observed. The plant may be a starting point for a race of triploid roses analogous cytologically to the pentaploid *Caninae*, or it is able to give either tetraploid or diploid offspring by self-fertilization. A third plant with over 90 per cent of the pollen sterile is suspected of being a triploid hybrid from *R. palustris* $\times$ *R. virginiana*.

7. *R. californica* and related species were found all to be tetraploid with fourteen pairs at diakinesis.

8. The tetraploid species examined cytologically nearly all exhibit irregularities during meiosis and also polyspory. They thus resemble hybrid forms in their cytological behavior.

9. Both tetraploid and diploid races morphologically similar were found in *R. subserrulata* Rydb.

10. The tetraploid forms often exhibit some rings of four chromosomes at diakinesis, but none have been found that are completely quadrivalent. It is concluded that they originated by duplication of diploid hybrids and have hybridized with each other.

11. The tetraploids are characterized by being able to flower on the season's turions and by a long flowering period. Many of them are semi-herbaceous or dwarf, and are believed to be recent or derived forms adapted to prairie and dry upland habitats.

12. *R. nutkana* and related species, and all but one of the specimens of *R. acicularis* and its varieties, were found to be hexaploid, with twenty-one pairs at diakinesis.

13. Hexaploids exhibit few meiotic irregularities.

14. All hexaploids in America apparently occupy one continuous range, and it is thought that they have not originated on this continent from a sterile triploid hybrid by duplication, but that they migrated from Asia as hexaploids spreading southward and eastward.

15. There are two parallel series of American Cinnamomeae, each consisting of hexaploid, diploid, and tetraploid types: (1) on the Pacific Coast *R. nutkana*, *R. pisocarpa*, and *R. californica*; (2) in the Mississippi Valley *R. acicularis*, *R. blanda*, and *R. suffulta*.

16. A specimen of *R. acicularis* from Alaska was found to be octoploid with twenty-eight pairs at diakinesis. The plant does not differ markedly from the hexaploid variety *lacorum*, but is distinguished by coming into flower earlier. It has pure pollen.

17. Examination showed that the hexaploids have a small proportion (under 10 per cent) of sterile pollen. Some diploid specimens have almost entirely good pollen while others have 10–15 per cent sterile grains. Most of the tetraploids showed 15–30 per cent sterile pollen, although individuals of *R. carolina* and of *R. virginiana* were found with 90 per cent of their pollen good. One tetraploid had 56–77 per cent of the pollen bad.

18. Good fruit was obtained after castration in one case only, that of a specimen of *R. blanda* (diploid) from Illinois which had 52 per cent bad pollen.

19. The flowering times of each of the large species groups are specific and characteristic when taken in relation to each other. The phenology of the species of American Cinnamomeae seems to coincide with phylogenetic relationship, those coming into flower first being the most primitive. The flowering order is: octoploids, hexaploids, diploids, tetraploids.

20. Cytological and morphological evidence support the theory of HARRISON and BLACKBURN of the hybrid origin of orthoploid series in *Rosa*. A possible origin of the North American polyploid series is worked out from this premise.

21. The presence of octoploid and hexaploid races of *R. acicularis* in America, and also of diploid and tetraploid races of *R. subserrulata*, is suggested as evidence in support of HURST's theory.

22. Cytological observations on American roses do not support HURST's theory of differential septets in *Rosa* which would require that sets of seven chromosomes separate together during meiosis. Extrusion is thought to be due partly to imperfect fixation and partly to disturbances consequent upon hybridization.

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EXPLANATION OF PLATES XVI-XIX

Except as otherwise stated, all figures were drawn with a Zeiss compensating ocular no. 20 and a 1.5 mm. apochromatic objective, with the aid of a camera lucida. They were reduced two-thirds in reproduction.

PLATE XVI

FIG. 1.—*R. bracteata* 3676, diploid; first metaphase plate, seven pairs.

FIG. 2.—*R. gymnocarpa* 4006, diploid; first meta-anaphase, seven pairs.

FIG. 3.—*R. pisocarpa* 4634, diploid; diakinesis showing three types of pairing.

FIG. 4.—*R. woodsii* 8152, diploid; early first telophase.

FIG. 5.—*R. salicetorum* 3530, diploid; early diakinesis with chain of six chromosomes.

FIG. 6.—*R. granulifera* 5925, diploid; two cells at diakinesis each with six pairs and two unpaired chromosomes, exhibiting distortion of nuclei and extrusion of chromosomes.

FIG. 7.—*R. hypoleuca* 8154, diploid; diakinesis, multipolar spindle.

FIG. 8.—*R. blanda* 3942, diploid; second metaphase plates.

FIG. 9.—*R. blanda* var. *hispida* 5771 (plant B), diploid; first meta-anaphase spindle with one pair off in cytoplasm.

FIG. 10.—*R. blanda* var. *glandulosa* 3753 (plant 5/N₃), diploid; somatic prophase.

FIGS. 11, 12.—*R. blanda* var. *glandulosa* 3753 (plant 2/N₃₈), diploid; diakinesis nuclei with two unpaired chromosomes and rings of two chromosomes.

FIG. 13.—Somatic prophase in root tip of semihardy, sterile segregate of culture 3753; fourteen chromosomes.

FIG. 14.—Fifteen chromosomes segregate in culture 3753 (plant 9/N₁); somatic prophase in parietal cell of pollen sac.

FIG. 15.—Plant 9/N₁, culture 3753, diakinesis; six pairs and three unpaired chromosomes; majority of chromosomes from contiguous cell in cytoplasm.

FIG. 16.—Culture 3753, plant 9/N₁, first metaphase; seven pairs and one univalent chromosome.

FIG. 17.—Culture 3753, plant 9/N₁, first metaphase; four bivalents and one univalent on spindle, three bivalents in cytoplasm.

FIG. 18.—Culture 3753, plant 9/N₁, sister second metaphases with seven and eight chromosomes.

FIG. 19.—Culture 3753, plant 9/N₁, sister second metaphases each with seven chromosomes; extra chromosome (?) on surface of shrunken protoplast.

PLATE XVII

FIG. 20.—*R. acicularioides* 8261, diploid; first metaphase with five bivalents and four univalent chromosomes.

FIG. 21.—*R. acicularioides* 8261, diploid; somatic prophase in integument.

FIG. 22.—*R. pyrifera* 6610, aneuploid; diakinesis, seven bivalent and two univalent chromosomes.

FIG. 23.—*R. pyrifera* 6610, aneuploid; diakinesis, seven pairs and one smaller eighth pair.

FIG. 24.—*R. woodsii* 4477, five young microspores produced from one sporocyte (ocular no. 10, objective 1.5 mm.).

FIG. 25.—Culture 3753, plant 7/N37, four megaspores (two superimposed) each with eight chromosomes, surrounded by archeosporium (ocular no. 10, objective 1.5 mm.).

FIG. 26.—Culture 3753, plant 7/N37, sixteen chromosomes in somatic prophase in cell from chalazal region.

FIG. 27.—Culture 2872, triploid; entering first metaphase, seven bivalent and seven univalent chromosomes.

FIG. 28.—Culture 2872, triploid; first metaphase, seven bivalent and seven univalent chromosomes.

FIG. 29.—Culture 2872, triploid; sister second metaphase plates with twelve and nine chromosomes.

FIG. 30.—Culture 2872, triploid; second anaphase spindle with fourteen large chromosomes (the halves of seven original bivalents) and eight others. This nucleus received seven univalents at first telophase, one of these has split, two are dividing longitudinally at equator, one lies at one pole partly split.

FIGS. 31, 32.—Culture 2872, sterile triploid; products of two microsporocytes ten cells from one and two large cells from the other (ocular no. 10, objective 1.5 mm.).

FIG. 33.—Culture 2949, triploid; twenty-one chromosomes at diakinesis, including four or five pairs.

FIG. 34.—Culture 2949, fertile triploid; late first anaphase, seven chromosomes at each pole (originally all paired), seven univalents dividing at equator.

FIG. 35.—Culture 2949, triploid; sister second metaphase plates, with fourteen and nine chromosomes (ocular no. 20, objective 1.8 mm.).

FIG. 36.—Culture 2949, triploid; somatic prophase in nucellus.

FIG. 37.—Culture 2949, triploid; somatic prophase in stylar cell, twenty-one chromosomes.

PLATE XVIII

FIGS. 38A, 38B.—*R. californica* 5849, tetraploid; cut cell at diakinesis, twelve bivalent chromosomes, ring of three and one uncondensed chromosome.

FIG. 39.—*R. brachycarpa* 5301, tetraploid; diakinesis, twelve pairs and a ring of four.

FIG. 40.—*R. aldersonii* 5367, tetraploid; sister second metaphase plates with fourteen chromosomes each.

FIG. 41.—*R. myriantha* 3537/B, tetraploid; fourteen pairs at diakinesis.

FIG. 42.—*R. obovata* 2651, tetraploid; late diakinesis, fourteen pairs (note condensed group of four).

FIG. 43.—*R. lyoni* 2883/A, tetraploid; late interkinesis, sister nuclei each with fourteen chromosomes.

FIG. 44.—*R. carolina* 5808/B, tetraploid; late first anaphase, two pairs lagging.

FIG. 45.—*R. carolina* 5808, ring of four chromosomes from cut cell at diakinesis stage.

FIG. 46.—*R. carolina* 5808, cut cell at first metaphase, ring of four and pair of chromosomes off in cytoplasm.

FIG. 47.—*R. serrulata* (*R. carolina* var. *glandulosa*) 3938, tetraploid; somatic prophase in stylar cell with twenty-eight chromosomes.

FIG. 48.—*R. carolina* var. *litoralis* 2654; seven cells the product of one microsporocyte (ocular no. 10, objective 1.5 mm.).

FIG. 49.—*R. rudiuscula* 4001, tetraploid; diakinesis, twelve pairs and one group of four; seven pairs with chromosomes more closely appressed and condensed.

FIG. 50.—*R. bushii* 3080, tetraploid; second anaphase, each grand-daughter nucleus receiving fourteen chromosomes.

FIG. 51.—*R. suffulta* 2682, tetraploid; two cells at diakinesis: one (cut) showing two rings of four, two unpaired chromosomes and seven pairs; other with eleven pairs and two unpaired chromosomes being extruded into next cell and two pairs left.

FIG. 52.—*R. suffulta* 2692, tetraploid; late diakinesis showing fourteen pairs, including condensed group of four chromosomes.

FIG. 53.—*R. suffulta* 5705, tetraploid; diakinesis with fourteen chromosomes fairly closely paired, chain of six, group of four, and four chromosomes loosely grouped in pairs.

FIG. 54.—*R. suffulta* var. *valida* 4459/A, tetraploid; late first anaphase, two pairs lagging much behind the others.

PLATE XIX

FIG. 55.—*R. subglauca* 3492, tetraploid; first metaphase plate with fourteen pairs.

FIG. 56.—*R. subglauca* 3492, tetraploid; first metaphase with twelve bivalent and four univalent chromosomes.

FIG. 57.—*R. subglauca* 3492, tetraploid; end of first anaphase, showing irregular distribution of chromosomes: twelve at one pole, one near equator, fifteen (including one split) at opposite pole, one small chromosome in cytoplasm (perhaps due to a univalent having divided at first anaphase).

FIG. 58.—*R. subglauca* 3492, tetraploid; second telophase, one spindle with thirteen chromosomes at each pole and one dividing at equator, the other with thirteen at one pole and twelve at other and one lagging chromosome; also one

split chromosome and four others off in cytoplasm. Extra chromosomes resulting from some univalents dividing at both anaphases.

FIG. 59.—*R. subserrulata* 6072, tetraploid; late first anaphase, ten chromosomes at each pole, three pairs and two univalents at equator, one of the univalents dividing.

FIG. 60.—*R. subserrulata* 6072, tetraploid; first telophase with two groups of seven chromosomes.

FIG. 61.—*R. subserrulata* 6072, tetraploid; first telophase with fourteen chromosomes.

FIG. 62.—*R. rudiuscula* 3501, tetraploid; meiosis in megasporocyte, sister nuclei showing fourteen chromosomes, one in interkinesis and other entering second metaphase.

FIG. 63.—*R. acicularis* var. *sayiana* 3754, hexaploid; early diakinesis, twenty-one pairs, four groups of two pairs.

FIG. 64.—*R. underwoodii* 8270, hexaploid; early diakinesis with sixteen pairs in main and five pairs in subsidiary nucleus.

FIG. 65.—*R. spaldingii* Ero, hexaploid; first metaphase plate with twenty-one pairs.

FIG. 66.—*R. macdougali* E8, hexaploid; five nuclei produced from one microsporocyte.

FIG. 67.—*R. acicularis* 6447, octoploid; diakinesis with twenty-eight pairs (ocular no. 20 and 1.8 mm. objective).

FIG. 68.—*R. acicularis* 6447, octoploid; first metaphase plate with twenty-eight pairs.



